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COMPETITIVE RELATIONSHIPS OF FOUR DIFFERENT LAWN GRASSES WITH FIELD BINDWEED AND DANDELION UNDER FREQUENT CLOSE CLIPPING[1]

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Considerable research has been done on the control of field bindweed (*Convolvulus arvensis* L.) in cultivated fields by the use of crop competition and intensive tillage. Little experimental work has been reported on the control of bindweed in lawns, parks, cemeteries, and other turf situations by crop competition or turf management. Kinch and Keim ('37) found hand removal of individual bindweed plants at intervals of 1 or 2 weeks, also treatment of individual plants with sodium chlorate, or repeated light broadcast applications of chlorate, to be effective but expensive methods of eradicating bindweed from bluegrass lawns. More recently the use of 2,4-D has been reported (Timmons, '47) to be partially effective in eliminating bindweed from turf.

The study reported here was undertaken in 1943 at Hays, Kansas, to determine the relative effectiveness of different lawn grasses in competing with bindweed under close clipping and differential watering practices. All plots were invaded by dandelion (*Taraxacum officinale* Weber) during the latter stages of the experiment, making it possible also to study the effectiveness of the different grasses and management practices in controlling this common turf weed.

MATERIALS AND METHODS

Native buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), Oregon Seaside bentgrass (*Agrostis palustris* Huds.), African Bermudagrass (*Cynodon dactylon* (L.) Pers.), and a local acclimated strain of Bermudagrass were selected for the study because of their ability to develop and to maintain dense sods under close mowing. The four grasses were planted by various methods suited to each April, 1943, on square rod (272.25 ft^2) plots in an area uniformly infested with field bindweed. The soil was a fertile alluvial silt loam which did not require fertilization or liming for optimum growth of grass. Buffalograss was tested under four different methods of management, bentgrass under two methods and the two Bermudagrass strains each under one method. The eight different combinations of grasses and methods of management are outlined in table I. Each was duplicated.

Buffalograss was watered as necessary for optimum growth in two methods and not watered in two methods. All other grasses were watered as necessary. One set of buffalograss plots and one of bentgrass plots were hand-weeded at intervals of two weeks during most of the first

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TABLE I. *The effect of different lawn grasses under various cultural treatments on the stand of bindweed and dandelion, 1943–1946*

Kind of grass and method*	Cultural treatment number of times			Plants per square rod** on various dates						
				Bindweed					Dandelion	
	Hand-weeded 1943 only	Mowed 1943–45	Watered 1943–45	5–17 1943	5–24 1944	9–25 1944	9–25 1945	9–2 1946	9–25 1945	9–2 1946
Seaside bent: watered as necessary, weeded	6	30	54	681	353	107	27	4	1363	1260
Seaside bent watered as necessary	0	30	54	773	560	128	25	0	1631	1954
Bermuda (coarse local strain): watered as necessary	0	29	19	640	625	166	2	0	1125	1321
Bermuda (African): watered as necessary	0	29	21	573	700	238	3	9	816	983
Buffalo: watered as necessary, weeded	5	25	20	516	450	28	1	0	438	434
Buffalo: not watered, weeded	7	23	0	527	482	107	3	4	102	129
Buffalo, watered as necessary	0	29	17	268	663	303	0	0	1613	1113
Buffalo: not watered	0	27	0	481	1038	585	124	59	284	242
None (bindweed check): not watered	0	26	0	—	1006	400	42	75	1450	—

* All plots were mowed to height of 1 inch every 2 weeks during growing season.
** Data are averages of duplicate plots.

growing season in 1943. During the remainder of the experiment they were mowed every two weeks. Otherwise, all plots were mowed to the height of one inch at intervals of two weeks during the growing season of 1943, 1944, and 1945. The mowing and watering schedules specified for the different plots were discontinued after 1945, but observations were continued during 1946 when all plots were maintained uniformly by mowing two inches high at frequent intervals without watering.

A sterile border two feet wide was established and maintained around each plot throughout the experiment by repeated applications of sodium chlorate. The chlorate-sterilized borders effectively prevented the grass and bindweed present on each plot from invading adjoining plots.

One-half of each plot was sprayed with 2,4-D at two pounds acid equivalent per acre, September 25, 1945, in order to determine the relative effectiveness of that chemical on dandelion in the various grass-soil moisture situations. Ammonium salt, sodium salt, ethyl ester and free acid formulations of 2,4-D were each used on one plot of each grass. The 2,4-D spray was confined to the sprayed portion of the plot through the use of a windboard.

Determinations of the stands of bindweed and dandelion were made at intervals during the four-year course of the experiment on the basis of plant counts in meter square quadrats. The quadrats were located by dropping a light weight iron frame in four or more places in each plot.

CLIMATIC DATA

Climatic conditions in 1943 were extremely unfavorable for production of satisfactory stands and growth of the grasses, especially on unwatered plots, but were unusually favorable in 1944 and 1945. The rainfall during the growing season (April–September) in 1943 was 12.82 inches compared to 17.42 for the 76-year average. The greatest deficiency was in April, May, and June, but July and August were also below normal. The

drought in 1943 was accompanied by abnormally high summer temperatures with maximums of 100° F or above occurring on 34 days during June, July, and August.

The growing season in 1944 was unusually wet and cool with a seasonal precipitation of 21.21 inches and only 11 days on which temperatures of 100° F or above were recorded. The rainfall for the growing season of 1945 was 17.46 inches and the season was cooler than normal with only 15 days on which temperatures of 100° F or above occurred. Rainfall in 1946 was above normal in May and September but deficient in the other months and totaled 17.38 inches for the growing season. The summer was abnormally hot with temperatures 100° F or above recorded on 27 days.

Results

Competitive relationships

Excellent stands of bentgrass were obtained in the spring of 1943 but the grass was low in vigor and killed out in spots during the extremely hot, dry summer despite frequent watering. The stands thickened up again in the fall and made complete ground cover. The two strains of Bermudagrass spread from planted stolons to a ground cover of 20 to 30 per cent by the end of the growing season in 1943. The buffalograss plots that were watered and hand-weeded started forming runners by June and developed a ground cover of 60 to 80 per cent by fall. The plots that were hand-weeded but not watered did not develop runners until August and attained a ground cover of only 25 to 30 per cent by fall. The buffalograss plots that were not hand-weeded but were mowed closely during the season emerged to good stands of seedling plants in the rows which were 12 inches apart, but developed only a few runners on the watered plots and none at all on the nonwatered plots.

The favorable growing conditions in 1944 caused nearly all of the grasses to develop a dense sod early in the season on most of the plots. The buffalograss that was neither hand-weeded nor watered in 1943 or 1944 developed a sod more slowly but eventually made a complete sod by late fall.

The data summarized in table I show chronologically the effect of grass competition and close mowing upon the stand of bindweed. It maintained or increased its stand during 1943 on most plots while the stands of grasses were becoming established. Bentgrass competed effectively with bindweed during the first season, especially where assisted by hand-weeding. During 1944 and 1945 the stand of bindweed decreased rapidly on all plots. After three seasons nearly all bindweed plants had been eliminated from the Bermudagrass plots and from the buffalograss plots that had been watered or hand-weeded. Less than 5 per cent of the original stand of bindweed remained on the bentgrass plots and only about 10 per cent remained on the buffalograss plots that had not been hand-weeded or watered. The stand of bindweed was further reduced on several plots during 1946. At the end of the experiment four of the eight grass-management combinations had apparently eliminated all of the bindweed and the other methods had given satisfactory control. Of particular interest is the reduction of more than 95 per cent of the stand of bindweed on a non-grass closely mowed check plot. This plot had become heavily infested with dandelion in 1944. Apparently the competition of dandelion with bindweed was about as effective as that of buffalograss on nonwatered, closely mowed plots.

Dandelion began invading the plots in 1944 but stand counts were not made until in the fall of 1945 when more than 1,600 plants were present on some square rod plots. Buffalograss kept out the dandelion much more effectively than did the other grasses, particularly where the plots were not watered. There were as many dandelions on the bent grass and local Bermudagrass plots as on the non-grass check, although the plants were

TABLE II. *Effect of 2,4-D treatment on dandelion and different lawn grasses, treatments made Sept. 24, 1945*

Kind of grass	Soil condition when treated	Dandelions per square rod, 1946*						% stand of grass
		Untreated		Treated		% of Untreated		
		4/29	9/2	4/29	9/2	4/29	9/2	4/29/46
Seaside bent	wet	1497	1607	285	467	19	28	5
Bermuda (local)	wet	1125	1321	109	696	10	50	100
Bermuda (African)	wet	1313	983	175	263	14	27	100
Buffalo	wet	1023	773	50	221	5	34	100
Buffalo	dry	488	185	61	15	14	6	100

* Data are averages of four plots, each treated with a different formulation of 2,4-D.

much larger and more vigorous on the latter.

Effects of 2,4-D

The results of the 2,4-D spray treatments on one-half of each plot in September 1945 are summarized in table II. The treatments killed 81 to 95 per cent of the dandelion with no significant differences in effectiveness on the weeds growing in different grasses or on wet or dry soil. However, reinfestation from dandelion seedlings and perhaps recovery of treated plants was much greater on plots that had been watered in 1943–45 than on those that had never been watered.

Little reduction in surviving bindweed plants due to 2,4-D spray was noted, probably because there were few bindweed leaves left below the mowing height at the time of the spray applications.

The 2,4-D treatment thinned out the stand of bentgrass 95 per cent but there was no apparent injury to the other grasses. In fact, these grasses showed much more vigor on the treated portions of the plots in the spring of 1946.

DISCUSSION AND CONCLUSIONS

Mowing to the height of one inch every two weeks removed the bindweed vine growth sufficiently to permit the seedling grasses to get started and eventually to develop a complete sod in all situations. After the grasses developed dense sods they appeared to force the bindweed to grow above the grass where usually it was clipped below the lowest leaf at each mowing. The subsequent elimination of most of the bindweed probably was due to root starvation caused by repeated complete defoliation. Observations of bindweed infestations in lawns and parks in the vicinity showed that the infestations persisted with undiminished stand and vigor in buffalo and bluegrass turf that was mowed to a height of two inches or higher, which left much of the bindweed growth undisturbed at each mowing.

Dandelion was observed to form a dense rosette of leaves at the surface of the ground. Much of the leaf surface remained uncut below the 1-inch height of mowing so that clipping every two weeks seemed to have no more detrimental effect —if as much—on dandelion than on the grasses. Probably the 1-inch mowing was favorable to the incidence and persistence of dandelion in these plots. This premise is supported by the observation by Kephart ('39) that mowing turf below two inches favors dandelions.

It appears that bindweed and dandelion cannot be controlled in turf by the same height of mowing. The high degree of effectiveness of 2,4-D on dandelion indicates that this herbicide could be used to supplement frequent close mowing for the control of both weeds in grasses that are tolerant to 2,4-D. Perhaps this chemical would also reduce the stand and

vigor of bindweed sufficiently to permit bluegrass and other grasses requiring higher mowing to compete more effectively with the weed.

Summary

Four lawn grasses were compared during 1943–46 in eight combinations of different grasses and methods of management on land heavily infested with field bindweed. All plots were mowed at a height of one inch at intervals of two weeks during the growing season each year.

Seven of the methods gave complete or nearly complete eradication of bindweed in 3 or 4 years and the eighth method reduced the stand more than 90 per cent in four years. Native buffalograss was the most effective of the four grasses tested where watered as necessary during periods of drought. Seaside bentgrass and two strains of Bermudagrass were only slightly less effective.

Grass competition under the frequent close mowing did not prevent dandelion from invading all plots and developing thick stands of 800 to 1600 plants per square rod on all watered plots by September 1945. Buffalograss afforded the most effective competition for dandelion, especially on nonwatered plots where an average of 100 to 300 dandelion plants per square rod were present.

Half of each plot was sprayed with 2,4-D in September 1945, which resulted in the elimination of 81 to 95 per cent of the dandelion on the various plots. The 2,4-D treatment reduced the stand of bentgrass 95 per cent but did not injure any of the other grasses. These showed increased vigor in 1946 on treated areas.

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CYCLE DOMINANCE AMONG THE FRASER SOCKEYE[1]

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"BIG" YEARS AND "OFF" YEARS

The first white visitors to what is now southwestern British Columbia encountered in the Fraser River one of the oddest of natural phenomena. Of the five species of Pacific salmon that entered this river to spawn, the commonest by far was the sockeye (*Oncorhynchus nerka*). In ordinary years these fish were abundant enough, but every fourth year they appeared in incredible numbers, greatly exceeding those of the years in between. The "big" year had occurred in this manner as far back as aboriginal memories extended, and it continued to occur until it met an untimely end in 1913. The mere abundance of these fish was not too great a cause for wonder, though it was remarkable enough. What really excited the imagination was the great disparity between the big years and the "off" years. Some idea of the actual magnitude of this disparity became apparent later on, when sockeye were exploited commermially. It was soon found possible to fish intensively enough, and to build canneries enough, to utilize some really substantial fraction of an ordinary year's run. However, up to and including 1913, when the dominant cycle last appeared, the utmost efforts of the cannery operators were insufficient to accommodate anything but a small percentage of its hordes of sockeye. In big years there was some increase in number of fishermen, but total fishing effort fell off sharply because at the height of the run each man fished relatively little. One drift of a gill net each day often sufficed to catch all the fish which a cannery quota system permitted a boat to sell (Babcock, '06). Many of the traps driven in Puget Sound were abandoned after the run was well under way. Often fish were caught on speculation, with only the smallest hope of finding a buyer, and later had to be thrown away. The periodicals of the time are full of complaints about the tremendous quantity of sockeye wasted for this and other reasons. Some even asserted that the number discarded exceeded the number of fish canned.

Because of this inability to cope with the myriads of fish available, statistics of the commercial pack of canned sockeye give only a pale reflection of the relative sizes of the big cycle and the other three cycles. Yet they are impressive enough. The figures given below apply to the period of maximum yield. The total Fraser sockeye pack made by Canadian and United States canneries is given in thousands of 48-pound cases, each case representing 12 or 13 fish (from Rounsefell and Kelez, '38, p. 759):

1904 cycle		1901 cycle		1902 cycle		1903 cycle	
1896	398	1897	1162	1898	468	1899	999
1900	402	1901	2082	1902	668	1903	372
1904	197	1905	1676	1906	368	1907	162
1908	250	1909	1688	1910	400	1911	192
1912	310	1913	2413	1914	538	1915	160
Average	311		1804		488		377

The average "big" year gave roughly 5 times as great a pack as the average "off" year. If one can believe the stories of the time, allowance for fish wasted would increase the total *catch* in big years to at least 7 or 8 times an ordinary year, perhaps more. But this still does not allow for the much smaller amount of actual fishing done in the big years. Attempts to correct for this involve a large element of guesswork, but it seems clear that on this basis the sockeye of the big years must have been *at least* 15 times as numerous as those of the other years. More

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probably they were 25 or 30 times as numerous, and possibly considerably more.

To get an idea of what this means in actual number of fish, one can postulate that fishing in the off years was rather intensive, taking say 75 per cent of the total stock. (Fishing of similar intensity in recent years has been shown to take 70–80 per cent of the stock.) The average catch of the 15 off years listed above was 392,000 cases, which, on the assumption just mentioned, corresponds to a total stock of 6,500,000 sockeye. The big years therefore had something of the order of 25 times this, or 160,000,000 sockeye.

What could possibly cause so great a discrepancy between one cycle and the other three? The basic condition was easily postulated and quickly confirmed. Like all Pacific salmon, the Fraser sockeye spawn only once and then die. Hence it seemed obvious that the sockeye of one big year were the parents of those of the next big year—in other words, the great majority of the individuals of these broods lived to be four years of age, from spawning to spawning. Early research fully confirmed this (Gilbert, '14) for in the big years more than 99 per cent of the fish were found to be four years of age. In the other cycles age IV fish were still in a majority, but age III and age V fish were present in considerable numbers, the latter averaging about a quarter of those sampled that were older than III. The III's were not representatively sampled by the fishery and no good estimates of their abundance are available for that period.

Careful study of individual spawning runs soon turned up other pertinent information. For one thing, it was found that the runs to separate spawning areas of the river were almost wholly separate entities. That is, each nursery lake had a race whose fish maintained a characteristic average size, color, time of migration and reproduction, size of eggs, age at maturity, and fingerling growth pattern (Gilbert, '16). In some instances a single lake had two or more separate races, differentiated by place and time of spawning, etc.; in general the spawning in rivers flowing *from* lakes was later than in other streams, because in them suitable temperatures occurred later in the year. Eventually an experiment was performed in which all the migrant smolts from a lake were marked in two successive years. In the year these broods returned as age IV and age V adults, it was found that all but 17 of the 2881 fish of those ages were marked ones (Foerster, '36). Evidently very little infiltration from other areas could have occurred.

Another interesting discovery was that the phenomenon of cycle dominance was particularly characteristic of the races of sockeye living in lakes situated above the canyon of the Fraser. There is a stretch of 125 miles or so of the Fraser, which includes the canyon, along which there are no tributaries that contain native sockeye runs (fig. 1). Hence is is convenient to divide the runs into "upriver" and "downriver" groups on this basis. All of the more important spawning areas upriver had a big cycle, and had it in the cycle of 1901. Since the upriver nursery lakes, taken together, are far more extensive than those below the canyon, this was sufficient to impress the dominance of the 1901 cycle upon the run to the river considered as a whole. Interestingly enough, most of the downriver nursery areas do not seem to have had a dominant cycle at all. It is true that records for several of these runs are fragmentary and inconclusive. However the Birkenhead River, Pitt River, Morris Creek and Cultus Lake were kept under fairly close observation because their runs were used as a source of eggs for the salmon hatcheries, and of these only Cultus Lake had a fairly well developed dominant cycle. But it was in the cycle year 1903, not 1901.

Having this general picture of the life-history of the sockeye, it is possible to make another estimate of the relative abundance of big years and off years by

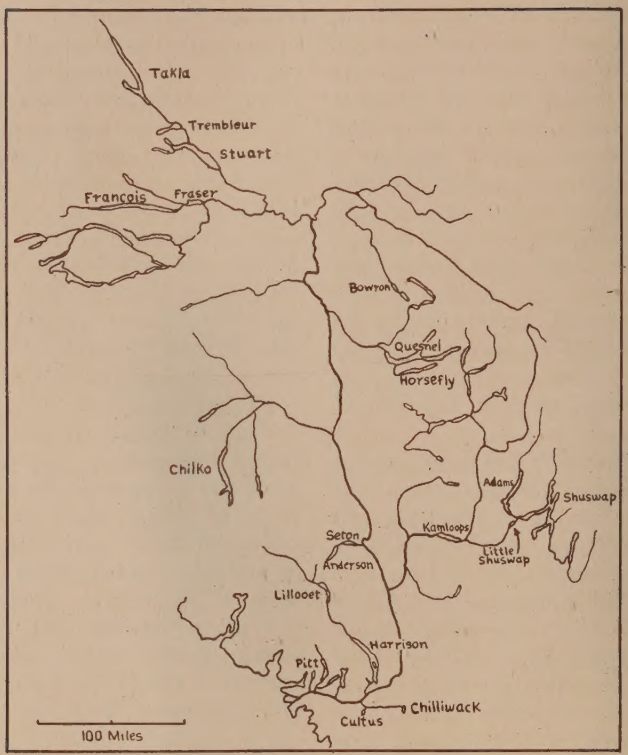

FIG. 1. Map of the Fraser River, showing the larger lakes. Lakes which currently support sockeye runs are named; unnamed ones are inaccessible because of natural or artificial barriers to migration. (For a detailed review of sockeye distribution, see Atkinson and MacKay's map in the 1943 report of the International Salmon Commission.)

using studies made just before the big years came to an end. Gilbert (1914–1919) sampled the commercial catch of Fraser sockeye over a period of years and determined the ages of the fish in the sample. It is usual to classify each fish both as to total age and as to the number of winters spent in fresh water, counting from the time of egg deposition in both cases. Thus a 4_2 sockeye, the commonest type, is four years of age at time of spawning and went to sea at the completion of two winters in fresh water (the first as an egg and the second as a fingerling). Neglecting for the present purpose all the more infrequent age types (3_2, 4_1, 5_3, 6_3, etc.), the fraction of 5_2 individuals among the group $(4_2 + 5_2)$ was 46 per cent in 1911, 10 per cent in 1912 and 15 per cent in 1914, an average of 24 per cent. In the big year 1913, on the other hand, only 9 specimens of 5_2 sockeye were found among 2,575 individuals of these two types, or 0.35 per cent. It does not necessarily follow that these figures accurately represent the composition of the *stock* in the corresponding year, since seasonal variations make representative sampling of the stock a difficult operation; however the sampling was done at much the same times through these years, so that the figures are comparable among themselves.

The importance of age composition for

our purpose becomes clear in the light of another discovery of Gilbert's, namely that the great majority of the 5_2 fish were destined for certain downriver spawning streams, particularly Pitt River, Morris Creek, two or three small tributaries of Harrison Lake, and to some extent the Birkenhead River (Lillooet Lake). Gilbert's estimates for 1916 are 80 per cent 5_2 fish at Morris Creek and Hatchery Creek (Harrison Lake), and a "large proportion" of 5_2's at Pitt Lake (1918, p. Q49); later Silver Creek (Harrison Lake) is included among those having predominantly 5_2 fish. In the same year Birkenhead sockeye were estimated to be about 25 per cent 5_2. In 1918 the 25 readable scales from 200 fish collected at Pitt Lake were almost all from 5_2 fish (one 6_3), and both these and the Morris Creek fish exhibited a length distribution equivalent to that of the 5_2 sockeye in the sample from the commercial fishery (1919, p. X31). Unfortunately a large majority of the scales from these two spawning areas were eroded so that age determination was impossible, and Gilbert points out that, with the procedure he used, age V fish tend to be overestimated as a result. Thus the above estimates for Pitt Lake and Morris Creek might be considerably in error unless unmentioned adjustments for this effect were made. For the 1918 Birkenhead fish, the quantitative effect of scale erosion upon the estimates was considered and the proportion of 5_2 individuals is set between 19 and 43 per cent, with a best estimate of 30 per cent. For our purpose it makes no difference whether or not the Pitt and Morris runs were really dominated by age V fish to the extent that they could be said to have a five-year cycle; what is significant is merely the fact that the downriver runs, considered as a whole, contained very important numbers of 5_2 individuals.

Upriver, on the other hand, 5_2 sockeye could scarcely be found at all in collections made from the Chilco and Quesnel runs, or from the Indian fishery on the Fraser itself. Only one collection containing any number of 5_2 fish was ever obtained upriver in 1916, 1917, or 1918. This was in a collection of 50 fish taken late in 1918 in the main river at Yale, which included 22 per cent of 5_2 fish. However, this was not representative of the whole run of that year. For the races which comprised the old big cycle, failure to produce 5_2 fish in appreciable numbers is sufficiently indicated also by the absence of 5_2's from the commercial catch of 1914 in anything exceeding ordinary numbers.

Having established the downriver provenience of the great bulk of the 5_2 sockeye, their occurrence in the commercial catch can be used as a standard against which the fluctuation of the 4_2 sockeye can be measured. These downriver races did not have any dominant cycle, though of course they fluctuated somewhat in numbers in an irregular fashion. The spawning-bed reports of Babcock (1911–1915) show that in 1913 the runs at Morris Creek, the Birkenhead River and the Harrison Lake streams were considerably larger than the average for that immediate period (as would be expected because of the reduced fishing effort in a big year), so that the relative scarcity of 5_2 sockeye in the 1913 commercial catch was not because of any sudden failure of these runs. If we estimate that the total abundance of downriver sockeye in 1913 was average, then the size of the total Fraser run in 1913 was to the adjacent off years as 0.35 to 24 (third paragraph above), or in other words the sockeye of the big year were 68 times as numerous as those of an average off year at that time.

A similar but less reliable estimate can be made from the relative numbers of "sea-type" or 4_1 sockeye found in different years—that is, those which go to sea as fry, spending very little of their active life in fresh water. The racial identity of this type was established by Gilbert, who in his surveys found them practically exclusively in the rapids of the

Harrison River, which again is in the downriver region. The original average representation of 4_1 sockeye in the fishery was about 2 per cent in off years and 0.04 per cent (1 individual) in the big year 1913 (Gilbert). On this basis the big year was about 50 times as large as the off years.

Certainly no great accuracy can be claimed for the estimates just given, for their sampling errors are obviously large. Because of random variation in sampling the age of the catch, at the 95 per cent confidence level the estimate derived from the 5_2 fish might be as small as 36 times the off years instead of 68 times as estimated; or, with equal probability, as great as 154 times. In any event these estimates do abundantly corroborate the picture of the fishery which was presented in an earlier paragraph, and suggest that in estimating the big years as 25 times the ordinary years we were quite likely being conservative. It should be noticed too that on the upriver spawning grounds characterized by big years, the discrepancy between big years and off years must have been considerably greater than is indicated even by these estimates, because in the off years at least half of the commercial catch came from downriver races. (If 24 per cent were 5_2's from downriver, the 4_2 sockeye from downriver must have contributed at least another 24 per cent.) Hence in the nursery areas actually involved, the sockeye produced by a big cycle can be conservatively estimated to have been of the order of twice 68 or about 130 times as numerous as those of the off cycles, on the average.

The Late Shuswap Runs

Up to 1913, the picture was one of a dominant 1901 cycle in all the important upriver areas, and an absence of dominance in most downriver areas. Since 1913 this picture has changed greatly. A succession of disasters almost obliterated the dominant 1901 cycle during the period 1912–1920, and reduced all the early upriver runs to a point dangerously close to extinction. First in importance, for the big run at least, was the obstruction of the channel of the Fraser canyon by rock dumped in during railway construction in 1912 and 1913, and by a large slide at Hell's Gate early in 1914. Prompt measures were taken to remove the accumulations of rock at various points but the work could only be done at the low water levels of winter and it was spring of 1915 before it was completed. Meanwhile the big run of 1913 had largely been prevented from passing upriver, as had the succeeding run of 1914 (Babcock, '14, '15). The run of 1912 may also have suffered, although, if so, it caused no comment at the time.

These spectacular occurrences distracted attention from another possible danger to the sockeye runs, an overdevelopement of the commercial fishery, which has been discussed by Rounsefell and Kelez ('38). Long before 1913 there was plain indication of a progressive decline in the yield of the 1903 cycle, which is reflected, for example, in the "index of abundance" computed by these authors (l.c., p. 772), or in the estimates of the actual magnitude of the stock given by Rounsefell ('49).[2] For the other two off cycles the decline in catch per unit of effort was much less striking, but a similar trend was suggested.

Following the years of the great canyon mortalities, the sadly reduced survivors got little immediate respite from fishing. The unprecedented prices offered for canned salmon during World War I and its aftermath resulted in a sustained tempo of exploitation, which finally collapsed only with the economic slump of 1921 and the simultaneous disappearance of most of the fish. It has also been urged recently that, contrary to the testimony of the engineers in charge, the re-

[2] Rounsefell makes no distinction between dominant years and off years in respect to the frequency and effectiveness with which the licensed fishing gear was used; hence his population estimates for the big years are much below what is suggested here.

moval of rock debris from Hell's Gate in 1915 could not have been complete and that this part of the canyon has remained a serious obstruction and cause of mortality (Thompson, '45). However the evidence for this has not been universally accepted, and the construction of fishways at the difficult points in 1944–45 was not followed by any significant increase in the rate of recovery of upriver runs until 1947, when a substantial part of the early fishing season was closed (Ricker, '47, MS).

The early 1920's were lean years for the Fraser sockeye, with the catch hovering around 100,000 cases per year. In 1926, however, there was a sudden upturn, which came from an unexpected quarter. A large stock of spawning fish appeared upriver late in the season in the Shuswap Lake region of the South Thompson branch of the Fraser—particularly in Adams River and Little River. Their number was estimated between 300,000 and 600,000 by different observers. The run four years earlier had been "good"—that is, by the standards then current—and later experience has shown that a badly depleted run will occasionally be estimated to increase as much as 10- or 15-fold in a single generation. Hence there need be nothing mysterious about the origin of this run, though many odd suggestions were offered at the time. This "new" run is of interest because it founded a new dominant cycle in Shuswap Lake and Little Shuswap Lake, and it is most instructive to follow its development. From the start it differed in two respects from the old big years at Shuswap. In the first place, it consisted exclusively of late-run fish, which were concentrated in lower Adams River and to a less extent in Little River, whereas the old run is said to have had more of its members among the early-run fish spawning in other streams. Still, the old big cycle did have a large late run in these rivers, so the new run was not without precedent in that respect. More interesting is the fact that the new dominant run was not in the 1901 cycle, but in that of 1902, showing that it was not any heritable characteristic which enabled the old big years to dominate the river.

For convenience the dominant cycle in any area will be designated "Cycle I," with the other three cycles following in order. The progress of the new dominant cycle and the associated "off" cycles at Adams River can be followed in the annual surveys of sockeye spawning in the Fraser, published in the Reports of the British Columbia Fisheries Department, and during recent years in the Reports of the International Pacific Salmon Fisheries Commission. Short quotations from these sources are given in an appendix to this paper. The basis of estimation appears to have been changed in 1946 and 1947 to include the fish in Little Shuswap Lake, so that comparisons with those years cannot be made on a completely comparable basis. Briefly, however, it appears that the dominant cycle of 1902 (Cycle I) now has in excess of 2 million spawners and is more than 10 times as large as any other. The two adjacent cycles come next with 200,000 sockeye in Cycle II and 64,000 in Cycle IV. In the latter instance the age III fish could be distinguished by size, and in 1945 the great majority were found to be of that age, hence were the product of Cycle I; only 1,150 were the "native" 4_2 sockeye actually spawned in Cycle IV. It is not known whether or not a similarly high proportion of age V (5_2 or 5_3) fish from the dominant cycle were included among the 200,000 estimated in 1947, the Cycle II year. Cycle III, which could contain very few if any fish from the dominant cycle, showed only 1,400 sockeye at last estimate. Thus in the two cases where they can be distinguished, the "native" or age IV sockeye of the present Shuswap off cycles are estimated to be at less than one-thousandth of the abundance of the dominant cycle.

In the light of this positive information from a specific area there need be no

hesitation about accepting our earlier estimate that the size of the stock in the old big years, in the areas where dominance prevailed, was of the order of at least 130 times as large as that of the off years.

What is most interesting about the late Shuswap run, however, is not that the off years are so small, but that *they have become small during the very period in which the dominant year has become large.* The dominant cycle grew from an estimated 20,000 or so fish in 1922 to more than 2,000,000 in 1942. At the same time the 1904 cycle, which was estimated to have 4,000–10,000 spawners during the late 20's and early 30's, reached a new low of 1,400 in 1944. The 1901 cycle produced only 1,150 age IV spawners in 1947, in spite of the existence of respectable runs during the 1920's from which a stock could have been built up. The 1903 cycle (Cycle II) has been larger than the other off years, on the whole, but its estimated 100,000 spawners of 1927 have made a very poor showing, having decreased to 17,000 by 1943; and although the estimate of the run rose to 200,000 in 1947 this may be partly a reflection of the new basis of estimation.

Evidently, then, one cycle has multiplied enormously while others have been reduced to commercial extinction! There is no apparent physical reason why this should have happened. Why should not all the off years at Shuswap Lake have increased at a rate comparable with the dominant year? Whether or not Hell's Gate was actually an important continuing obstacle to early-season sockeye runs, this was certainly not true toward the close of the season when the Shuswap run was passing through. At that time of year the Gate rarely presented any difficulty (Thompson, '45, fig. 54). During the period 1924–1946 there were only four years during which "unfavorable" water levels prevailed for more than a few days at a time during the latter part of the season, and one of these years has occurred in each of the four cycles, including the dominant one. Thus the dominant cycle has had no advantage over its associates in respect to possible migration hazards. It may be noticed too that none of the runs to other upriver areas have exhibited a net decrease over the same period, in any cycle, and many have shown very substantial gains.

It is true that in one respect the present dominant 1902 cycle at Shuswap has had an advantage over *two* of the others—the advantage of being in an even-numbered year. The advantage consists in the fact that pink salmon (*Oncorhynchus gorbuscha*) are abundant in Puget Sound and the Fraser River in odd-numbered years only, and this makes for much more intensive salmon fishing late in the season when they are running. In even years, therefore, a late-running race of sockeye like that to Adams River is considerably less heavily exploited than in odd years (Rounsefell and Kelez, '38). This advantage was particularly important at the time when the present dominant cycle was still small and unable to attract many fishermen on its own account. It is because of this fact, quite probably, that the new dominant cycle was developed in even years instead of continuing in the old 1901 cycle. Yet this effect cannot explain much or any of the *present* size difference between the dominant 1902 cycle and the others, because the 1904 cycle also occurs in even years and it now numbers less that 2,000 fish!

Possible Causes of Cycle Dominance

While it would be too much to say that the causes of cycle dominance are well understood, it is possible to point out what kinds of explanation are acceptable and to offer some specific suggestions. The old big cycle had persisted through many decades of the historical period and for an undetermined period previously. Right up to the time it was accidentally destroyed it showed no sign of diminishing its domination of the river. This fact at once suggests that the big cycle

somehow was acting unfavorably upon the off cycles, and actually prevented them from becoming numerous. Such a view receives striking confirmation in the story of the development of the present dominant cycle at Shuswap. There we have plain indication of the cut-throat competition which exists between a dominant cycle and the other three. "Competition" is perhaps scarcely the word for it, since the weak cycles apparently never had a chance, and two of them have been reduced almost to the vanishing point. Obviously then the only satisfactory explanations of dominance will be those which involve some kind of interaction between the dominant cycle and the others —interaction which must be favorable to a larger cycle (at least above a certain minimum size) and unfavorable to smaller ones.

In searching for mechanisms whereby the dominant cycle might suppress the others, we must enquire first whether the interaction between them occurs in fresh water or in salt. The complete synchronization of the former big years of the various races upriver into the 1901 cycle might have suggested the ocean as the likely place to look. However, since the destruction of the old big years there has arisen a diversity of cycles in existing and incipiently dominant runs upriver, as will be described later. This almost certainly rules out marine competition as a causal mechanism. Such competition should affect all runs in the same cycle, for it is very difficult to imagine that each race of sockeye has its own ocean home where it can remain aloof from its neighbors, when they are mixed together during both the outward and return migrations. Similarly the customary absence of dominance downriver, and the former existence of a dominant 1903 cycle at Cultus Lake, make it impossible to postulate a single interaction involving all runs together. Finally, if serious ocean competition existed, we should expect it to be reflected in sharp variations in the size as well as the abundance of the fish produced in different cycles, whereas Gilbert's measurements in successive years from 1911 onward show only very small year-to-year differences among either the commercial or the spawning-ground samples. This leaves the lakes as the most logical location for inter-cycle competition, and hence for an answer we must look to studies of the ecology of the sockeye in fresh water.

As described earlier, young sockeye normally spent a full year in a lake, to leave it for the ocean the following spring. A usually small but rather variable number of them remain in the lake a second year and then migrate, becoming the adult fish designated by the subscript "3" (mostly 5_3, rarely 4_3, 6_3 or 7_3). At Cultus Lake it was found that still others never leave the lake at all, even though they are offspring of anadromous parents. Instead they remain in the lake two, three or four years and mature there as "residual" sockeye. Thus in the nursery lakes there are opportunities for both direct and indirect interactions between the different cycles, and both types have been proposed.

1. *Inter-cycle predation.*—Foerster ('44) observed at Cultus Lake that there was an unusually large fraction of the brood of the dominant cycle and of Cycle II which failed to go to sea at the end of a year in the lake. For the most part, apparently, these fish left a year later, but some considerable number became residual cockeye maturing in the lake. Although the great bulk of sockeye food is plankton, there is a good possibility that these older sockeye, particularly after they have lived for two growing seasons, can consume young sockeye fry of later cycles. This has not yet been observed, but residual sockeye of two years of age have been found to eat young fish of other species, so there is little reason to doubt that they can consume sockeye fry. Whether they could do so in quantities sufficient to have a controlling effect upon the weak populations is not yet known, but it seems very likely. Similar effects

have been observed by Thompson ('41) among crappies (*Pomoxis*) and by Ricker ('42) among bluegills (*Lepomis macrochirus*). Under favorable conditions a large spawning of these fish produces a brood which consumes the progeny of later broods so completely that practically no successful reproduction takes place again for a period of 3 to 5 years, or after the big brood has mostly died off. The bluegill is of especial interest in this connection because, like the sockeye, it is not ordinarily a fish-eating species.

2. *Competition between cycles for food.* —The suggestion was early made that a dominant cycle might exhaust the sockeyes' food supply so severely that it would take a lake three years to recuperate in this respect; hence the poor runs of the off years. In this crude form the hypothesis evidently has little probability, particularly since it has been shown that sockeye food organisms were present in Cultus Lake in much the same numbers of two years of small sockeye populations as in a year of large population. In the year of large population the abundance of *Daphnia* declined earlier in the summer than in the other two years (Ricker, '37), suggesting a real possibility of depletion of food supply by a big brood, but there was no sign of any carrying-over of this condition to ensuing years.

There is a possibility, however, that food competition is really serious only during some limited period in a restricted zone of the lake, which might not be detected by general plankton sampling. Foerster (1944) found that the yearling migrants at Cultus were of much smaller size in the dominant cycle than in other years (table I) and the suggestion was made recently that an upper limit to the abundance of the *dominant* populations might be set by the starvation of many of their members at a very early age (Ricker and Foerster, '48). In a somewhat similar way the very young fish of the broods *following* a big year might be affected by food competition with the non-migrating members of the dominant Cycle I.

TABLE I. *Estimates of the Cultus Lake yearling crop (migrants plus non-migrants, but excluding those which would have or did become residuals), the average weight of these yearlings and the percentage of non-migrants among them, arranged by cycles.* (From Foerster's data; see Ricker and Foerster, 1948, table 1)

Cycle	Year of spawning	No. of yearlings (*thousands*)	Ave. wt. of yearlings (*grams*)	Percentage of non-migratory yearlings
I	1927	3,092	2.8	22
I	1931	2,204	3.0	29
II	1928	91	4.6	57
II	1932	263	5.2	54
III	1925	200	8.0	8
III	1929	352	7.1	1
III	1933	246	7.6	2
IV	1926	419	4.7	20
IV	1930	788	7.3	0
Averages				
I		2,648	2.9	26
II		177	4.9	56
III & IV		401	7.0	6

The fingerlings of Cycle II are exposed to the competition of those members of Cycle I which go to sea at two years of age, as well as those which never go to sea. However, for Cycles III and IV to be importantly affected by either predation by, or food competition with, the dominant cycle, it would be necessary that some rather large number of non-migratory sockeye be present in the lake. Indeed it was the discovery of the existence of "residual" sockeye which first made significant predation and food competition among all cycles seem possible, and led directly to the suggestion that the causes of cycle dominance might be looked for there (Ricker, '38). Unfortunately, no observations have ever been made upon the residual sockeye produced by a really large dominant population. The largest year-class which was studied at Cultus Lake was that of 1931, whose effective parental population was about 30,000 (there were 38,000 spawners that year, but some eggs were taken artificially and removed to other watersheds). This year-class produced the largest number of residual sockeye yet observed, though

there is no way of knowing whether they might have been numerous enough to control effectively the abundance of later broods, since no estimate of their absolute numbers is available. To judge from the 38 individuals taken in a single set of a gang of gill nets in October, 1934, the number maturing at age III must have been at least several thousand, and might have been ten to twenty thousand. It might well be that the slower growth of the larger year-class of 1927 (from 82,500 spawners) would have deflected a very large number of young from migrating to sea, and so produce a body of lake-living sockeye that would dominate the lake for three years. Growth studies showed that the residual sockeye were recruited mainly from among the slower-growing members of a year-class (Ricker, '38), and really slow growth might swell their numbers disproportionately.

There is one aspect of Foerster's ('44) data on growth and survival of young sockeye in Cultus Lake that is of interest in this connection, namely the fraction of non-migrating yearlings produced in the different years. As shown in table I, the dominant or Cycle I years were estimated to have about 26 per cent of their sockeye fail to migrate during the first spring after hatching. (The figure would be increased by adding the unknown number of yearlings destined to become non-migratory residual specimens.) This 26 per cent is greater than the non-migrants of most other years, and is doubtless to be associated with the observation just mentioned, that within any given year-class slow growth favored delayed migration [3] or no migration at all. What is more remarkable, in table I, is that *Cycle II* produced an even larger proportion of potential two-year-old migrants—56 per cent—whereas other non-dominant cycles average only 6 per cent. The significance of this can scarcely be assessed without further observations. It is probable, for example, that Cycle II is the one most affected by competition for food with the surviving members of the dominant cycle, and it may be that this slows down the growth of the fingerlings particularly during some time of life which is rather critical for the determination of migration or failure to migrate. The *total* first-year growth of the fingerlings of Cycle II averages less than that of Cycles III and IV, although it is superior to that of Cycle I (table I). Whatever may be the correct interpretation of these observations, they well illustrate the lability of the migratory behavior of the sockeye, and its susceptibility to modification by physiological or environmental changes induced by the presence of a dominant year-class.

3. *Activity of predators.*—The work on predacious fishes at Cultus Lake led to a suggestion that the piscivorous fishes of a lake might play a role in dominance (Foerster and Ricker, '41). Squawfish, char, trout, and other sockeye-consuming fishes are certainly unable to vary in abundance from year to year as abruptly as do the sockeye. Yet the latter may constitute their principal food (Ricker, '41). In such a situation the general level of predator abundance would be determined, directly or indirectly, by the

[3] However the old dominant populations upriver did not produce any appreciable fraction of two-year-old migrants. From the spawning of the big year 1909 Gilbert found only 79 examples of 5_3 sockeye among 2,389 whose complete age history was determined in 1914, and in general the adults of that and earlier Cycle II years were not much more numerous than those of the other off cycles. This suggests that at very high population densities the great majority of the non-migrating yearlings become lake-living residual fish. It is interesting that the dominant cycle of one of the runs upriver did produce some considerable quantity of two-year-old migrants *when its abundance had been much reduced* by the canyon obstructions of 1913 but was still considerably in excess of that of the off cycles. Gilbert's samples from the Chilco run in 1918 were 35–40 per cent 5_3 (as compared with 6 per cent 5_3's in 1916, the only other year available). At this intermediate level of abundance the dominant Chilco cycle may have been comparable to the dominant cycle at Cultus Lake, and it evidently behaved in a similar manner as regards migration.

size of the smaller sockeye populations, and might in turn determine *their* abundance by way of some kind of predator-prey interaction. Any sockeye population which by chance came to considerably exceed this size might gain some relief from predation. If so, it could increase, as a result, outside the bounds of control by the predator populations, the latter being held back by the necessity of staying alive on the slender rations provided by the sockeye of the off years.

The principal difficulty with this hypothesis is that while it might explain how a big year could increase, it does not suggest any reason why the smaller years should decrease, as was observed at Shuswap. In addition, it is not clear why there should be only one big cycle on this basis; two would seem quite feasible, occurring in alternate years. It should be mentioned too that at Cultus Lake predacious fishes consumed sockeye almost strictly in proportion to their abundance, up to the largest sockeye population densities observed; so that under the conditions observed there, the abundance of sockeye of a future dominant cycle would have to be raised *by other means* beyond the level of the 1931 sockeye population, before any relief from predation would be gained. However, even though it may seem unlikely that predator-prey interactions could initiate dominance, they may well play some role is developing it to the extreme stage which it sometimes assumes.

At this point hypothesis must rest for the moment. Perhaps one of the above three suggestions can be modified to suit all the known facts, but more probably some combination of them will be necessary. On the basis of what data are now at hand it would be tempting to postulate that food competition between age 0 sockeye of Cycle I and age I sockeye of Cycle II is the more important effect during the first post-dominant year, while predation by age II and age III residuals of Cycle I upon the age 0 sockeye of Cycles III and IV is more important in the two following years. This would be in accord with the observation made at Cultus Lake that Cycle II fingerlings had a slower rate of growth than those of Cycles III or IV, and it would suggest a possible reason for the fact that at Shuswap Lake Cycle II has remained more numerous than Cycles III and IV (unless it will be found there that Cycle II now consists largely of age V fish). Naturally it is quite possible that still other types of interaction exist. One may wonder, for example, whether some significant role may not be played by the populations of kokanee or "land-locked" sockeye which are abundant in some lakes. Observations on the sockeye populations of Shuswap Lake and of lakes now in process of developing dominance could supply critical information.

Whatever the exact causal mechanisms may prove to be, observations to date very strongly indicate that under natural conditions a really large sockeye population can live in a lake in only one year out of four. This possibility has been rather slow to gain recognition. During the early 1900's J. P. Babcock and others confidently predicted that suitable regulation of the fishery, supplemented by artificial propagation, would eventually produce typical "big" runs in all four cycles, and he seems never to have abandoned this view. Even so astute an observer as Gilbert was of the opinion that "any method which might be successful in re-establishing it [the big year] would be equally successful in raising the traditional lean years of the Fraser . . . to an equality with the old-time 'big years'" ('21, p. 28). Possibly these men were influenced by a theory of dominant cycles which appears in the early literature and which, if true, would make four big cycles seem quite feasible. This theory postulates prehistoric rockfalls or similar natural catastrophes in the river, which were supposed to have reduced the abundance of sockeye in all cycles but one. Although even its proponents seem to have been little satisfied with this suggestion, it may

be well to enumerate the objections to it. 1. It is inherently very improbable that an accidental obstruction would persist for three years, then suddenly vanish and allow the fourth cycle to pass. 2. It is impossible that such an event could have affected the Cultus Lake run downriver and produced dominance there, for the lake lies only 50 feet or so above sea level and the slope of its outlet stream is gentle. 3. In the development of the new dominant cycle at Adams River there is no indication of catastrophes affecting the off years. 4. Finally, even if some accidental disturbance in the river could *initiate* cycle dominance, it could not account for its continued existence scores or hundreds of years later. In the absence of inter-cycle competition the maldistribution of abundnace would soon be corrected, when its cause disappeared, by the action of the ecological principle that large populations tend to have lower rates of reproduction than ordinary-sized populations.

Synchronization of Dominant Runs

If the primary cause of cycle dominance is to be found in conditions which develop independently in each nursery lake, there is still the problem of accounting for the former synchronization of the dominant runs throughout the upper Fraser. Because dominance appears to be self-perpetuating, it is only necessary to suggest conditions under which they could have become synchronized *once*. This evidently takes us back to the history of the establishment of sockeye in the Fraser watershed following the ice age. Geologists tell us that the whole of the present Fraser drainage was ice-covered several times during the Pleistocene, except for the higher mountain peaks. During early post-glacial times the lower Fraser valley was flooded to a depth of several hundred feet (Burwash, '18), so the various races of sockeye in lakes tributary to it could have entered these lakes almost directly from salt water in most cases. The original colonizers were presumably stray sockeye from lakes on Vancouver Island, Puget Sound, or the Olympic Peninsula.

Between these lakes of the lower river and Seton Lake, the first upriver lake suitable for sockeye, there stretch 90 miles of the Fraser canyon—a V-shaped valley extending from Hope northward. During the glaciation this trough was, of course, filled with ice, but it never contained a valley glacier and so retained its youthful contours and steep gradient. It would be a remarkable feat for home-loving sockeye to ascend this long stretch of fast water and establish new settlements above. Actually it is not at all certain that they did so. During early postglacial time much of the interior drainage of British Columbia that now lies in the Fraser watershed was tributary to the Columbia River, through the broad low valley connecting Okanagan Lake with the Shuswap River at Enderby. If the timing were correct, the present upper Fraser drainage might have been colonized by that route.

From whatever source the fish came, the initial stages of colonization of the present upper Fraser lakes must have been haphazard and uncertain. As mentioned earlier, sockeye are strongly inclined to return to their native streams, so that wanderers are in a very small minority. For a new lake to be colonized successfully, it was necessary for errant sockeye of opposite sexes to reach a favorable new spawning ground in breeding condition simultaneously, and for their offspring to return to the new site in some numbers. Though improbable in any one year, over a long period of years such an event becomes almost certain to occur. The improbability, however, indicates that only one upriver lake was likely to be colonized in any given decade, say, even if two or more should happen to have been opened up simultaneously. In the favored lake, at first the run to only one cycle would be established. Though age III and age V individuals would presumably soon "seed" the other

cycles, the internal mechanism making for dominance would ensure that the original cycle retained a commanding position. This new run would itself soon contribute wanderers to other areas, and these would be most numerous, by far, in the dominant cycle. What would be more natural, then, than that other available lakes would have *their* initial seeding in the same cycle, and that the dominance of this cycle would thus be propagated, finally, throughout the whole of the upper river? Of course, some lake somewhere *might* get a start from one of the off cycles, and if it did, there would be no reason why its dominant cycle should not develop and be maintained in a year that was out of step with the majority. But as a matter of fact no such lake was known above the canyon, or at least I have found no record of it.

There remains the question of why dominance was not and is not developed in most of the lakes of the lower Fraser. Perhaps a clue may be found in the relative availability of good spawning grounds. Sockeye usually spawn in streams, though they sometimes can find suitable lake gravels. In general, lakes of the lower river are glacial troughs situated in the rugged terrain of the Coast Range mountains, and neither they nor their tributaries are well provided with good spawning beds. The smaller streams tend to dry out near their mouths in summer and early autumn, and the heavy autumn and winter rains produce floods than can bury or wash out a season's spawning. The larger and more permanent streams in this region, like the Pitt River above Pitt Lake, tend to have bottoms of coarse rounded stones among which even the hardiest sockeye may have trouble in excavating a nest.[4] It may be suggested therefore that these downriver lakes have not developed a dominant cycle simply becouse they lack spawning beds sufficient to support a big run. At least it seems obvious that Harrison Lake, for example, has never had spawning accommodation for runs at all commensurate with its size. The much smaller Lillooet Lake had and still has much larger runs, presumably because the Birkenhead River above it flows through a flatter and drier terrain, verging on that characteristic of the "Cariboo" district of interior British Columbia, and is accordingly much better supplied with gravel reaches. Cultus Lake, containing the downriver race which did develop a dominant cycle, has poor spawning streams but its sockeye spawn in the gravel of several creek deltas that have been built out into the lake. The small size of the lake makes these sites much more extensive, in relation to the total water area, than is the case in any of the other downriver lakes. Even so, dominance at Cultus Lake apparently never took the extreme form that oc-

[4] As a matter of fact a race of sockeye does spawn successfully in some limited parts of this stream and it is interesting that it consists of fish which have about the largest average size of any in the whole river system. The principal rival claimants for this honor are the Morris Creek sockeye, whose spawning beds are almost equally coarse. According to Gilbert's observations the large size of both of these races is at least partly the result of their frequently spending three growing seasons in the sea, instead of the usual two. Possibly, therefore, in these races size and even age at maturity has been hereditarily modified as an adaption to conditions of existence. That is, large size would be more favorable for excavating nests among the coarse gravels and stones which they are compelled to use for spawning.

Another interesting apparent adaption is found in the Harrison Rapids race of sockeye. As noted earlier, this is the only race whose fish are habitually of the 4_1 type, that is, go to sea as fry. Robertson ('22) shows that these sockeye have much the largest eggs of any race that has been investigated, though the spawners themselves are the smallest in the whole river! It appears therefore that this race is varying in the direction of those species of salmon which consistently go to sea as fry. These latter are the chum and pink salmons (*Oncorhynchus keta* and *O. gorbuscha*), both of which are noted for their large eggs. One must imagine that large eggs, and hence large fry, are especially advantageous when the young fish must go to salt water shortly after their free-swimming life begins—sufficiently so to compensate for the correspondingly smaller *number* of eggs which each female can mature.

curred and still occurs in some of the upriver lakes. The ratio of its dominant cycle to the smallest weak cycle was of the order of 10 or 20 to 1, not 100 or 1,000 to 1.

Dominance in Other Runs

If we define a dominant cycle as one which has runs sufficiently abundant to inhibit the increase of the smaller cycles which accompany it, then only at Shuswap Lake is there a well-developed dominant run at the present time. However, since there is some reason to suppose that all of the areas which formerly had dominant cycles will sooner or later have them again, it is of interest to see what stage of development each of them has reached.

Chilko Lake.—The recuperation of the Chilko run began to attract attention in the late 1920's, shortly after the Shuswap run did. The following estimates of its abundance are from the reports of the B. C. Fisheries Department (for the years 1928–1940) and from those of the Salmon Commission (for 1941–1947):

1904 cycle		1901 cycle		1902 cycle		1903 cycle	
1928	20,000	1929	70,000	1930	900	1931	2,500
1932	70,000	1933	100,000	1934	3,500	1935	2,500
1936	74,000	1937	110,000	1938	7,000	1939	3,400
1940	350,000	1941	464,000	1942	34,000	1943	13,500
1944	329,000	1945	193,000	1946	60,000	1947	55,000

There are two Chilko cycles which are currently large enough to be of major importance to the commercial fishery, those of 1904 and 1901. The last-named of these immediately follows the first, and it originally had the larger population, but recently it has taken second place. Since the other two cycles have continued to increase, neither 1904 or 1901 can properly be called a dominant cycle as yet, though they are probably close to that point.

It may be that considerable significance should be attached to the fact that at Chilko the 1904 cycle has recently overtaken that of 1901. The latter suffered, in 1945, a decrease from 464,000 to 193,000 spawners. This was an unexpected reverse which, interestingly enough, occurred nowhere else upriver but at Chilko in that year. The 1904 cycle at Chilko Lake had been only one spawning behind the 1901 cycle in its recovery, and in 1940 it achieved about 350,000 spawners. If we assume that at that point it became large enough to play a decisive rôle in the interactions between cycles, then the unexpectedly poor showing of the progeny of the spawning of 1941 could be attributed to the unfavorable influence of their immediate predecessors of 1940. In the light of our hypotheses of inter-cycle competition or predation, enumerated earlier, it seems likely that the *later* of two adjacent nearly-equal cycles would be at a disadvantage. On that basis we should look for the 1904 cycle to continue to increase and to assume dominance at Chilko in the near future, and for the 1901 cycle to fall off gradually, just as did the off cycles at Shuswap. Whether or not this is so, it cannot be expected that *both* the 1904 and the 1901 cycles will remain abundant indefinitely. Their development during the years immediately ahead will provide an excellent test of the soundness of our interpretation of dominance in general.

Quesnel Lake and Horsefly Lake.—The run to the Quesnel area is an early one and is currently one of the smallest in relation to its former abundance. It has, however, retained a nucleus of spawning fish in the 1901 cycle—the old dominant cycle—which in 1945 numbered 3,000. All the other cycles had less than 100 fish at the latest estimate. Barring unexpected catastrophes, this should mean that a new dominant run in the 1901 cycle will quickly grow up, eventually to include at least one million spawners out of the several millions which it is said to have had formerly, the remaining millions to go to the fishery. With continued closure of the early fishing season, such as was inaugurated by the Salmon Commission in 1946, this may well be ac-

complished in a matter of three or four generations.

Fraser Lake and Francois Lake.—Most of the spawning in this area is in the Stellako River between the lakes. The largest run is in the cycle year of 1902, and it achieved 245,000 spawners in 1946. Next is 1904, with 56,000 in 1947, the other two cycles being smaller (IPSFC reports). The 1902 cycle is so far ahead that it seems likely to establish its dominance, though there is no evidence that this has been achieved as yet—that is, the off cycles were still increasing during their most recent generation.

Stuart, Trembleur and Takla Lakes.—The runs in this region are divided into an early group and a later group, the former migrating at the start and the latter during the middle of the Fraser fishing season. Recent estimates, from IPSFC reports, are as follows:

	Early runs	Later runs
1941	6,300	5,500
1942	8,200	"present"
1943	3,000	scarce or absent
1944	400+	20+
1945	28,200	23,600
1946	9,500	500
1947	14,200	60

Both the early and the later runs are now most numerous in the old big cycle year of 1901, but only among the later group does this cycle have a commanding lead.

Other upriver areas.—The Reports of the Salmon Commission show that runs to the Bowron area numbered 2,000–7,000 through 1946, with no indication of dominance; in 1947 closure of early fishing brought 24,000 spawners to this region. Runs spawning in Raft River and Finn Creek, whose lake life is presumably spent in Kamloops Lake, number a few thousand spawners at most. It is possible that the limited spawning grounds available in this area are not sufficient to support a dominant run, and I have found no definite statement that either Raft River or Bowron formerly had dominant runs.

Two other areas, however, definitely did have dominant runs prior to 1913: Adams Lake and the Seton-Anderson system. Of these Seton-Anderson, like Shuswap Lake, formerly had both an early and a late run, but it now has very few spawners of any kind, in any cycle. The run to the Adams Lake tributaries was formerly largely or exclusively an early one, and no sign of this now exists. Late-run fish did enter the lake in 1942 and to a less extent in 1946, but these are probably a sort of "overflow" from the abundant spawners of the 1902 cycle in Adams River immediately below it.

Cultus Lake.—The former dominance of the 1903 cycle in this small downriver lake has now become completely unrecognizable. The 1903 cycle produced 82,500 spawners in 1927 and 38,000 in 1931, by actual count, as compared with off cycles of 5,000–10,000 during that period. Largely because of a general change in the economy of the lake by an experiment in control of piscivorous fishes, the 1904 cycle became as numerous as the formerly-dominant 1903 cycle, and with the cessation of control work both decreased together.

Distribution of Catches among the Cycles

The question of dominant cycles is not without its practical aspects. The early division of the Fraser fishery into big years and off years was economically very undesirable. The canneries available in 1913 were unable to process the the runs of the good years, but were considerably in excess of the requirements of the poor years. To use the big runs to capacity would have meant a big outlay for additional facilities that would have had to lie idle three years in four. This, of course, makes for higher costs, and the obtaining of a greatly increased supply of seasonal labor, one year in four, also presents problems. In addition, in the early years the financial burden of unused capital outlay constituted a constant inducement to overfish the off years, which of course aggravated the situation further.

To obtain a more even distribution of

the Fraser sockeye stock throughout the four years, two approaches are possible. Either an attempt could be made to develop runs of more or less equal abundance among the four cycles in each spawning tributary, or the dominant runs of different lakes could be distributed more or less equally among the four cycles. Considering the strong natural forces making for dominance, as illustrated at Shuswap Lake, the latter course will probably be easier. Indeed some progress has already been made. Currently there is a dominant 1902 cycle at Shuswap Lake, and the 1902 cycle at Fraser Lake seems well on the way toward that status. The 1901 cycle is leading in the Stuart Lake and Quesnel Lake region. Neither of these latter had, in 1945, a run large enough to make any considerable contribution to the fishery, but the potentialities of both areas are very great. At Chilko Lake both the 1901 and the 1904 cycles currently have rather good runs, and it was shown above that there are some grounds for anticipating that 1904 will soon predominate in that area, though this is not yet assured. Only the 1903 cycle appears to be completely an orphan. It currently lacks a dominant run, and does not seem to be leading the field in any important spawning area, although in most of them it has a good nucleus for possible future expansion. No permanent expansion will be possible for it, however, if dominant runs of other cycles are allowed to develop in all the available areas.

There are two or three ways in which the 1903 cycle might be given a boost. The Seton-Anderson Lake system, and also Adams Lake, should be able to support large sockeye runs and at present have very few. Attempts could be made to develop a 1903 cycle in them by transplantation of eggs from other areas. If this did not work out as planned, it would probably be possible to suppress an already-existing dominant cycle in some major spawning area and divert its productive capacities to the 1903 cycle, simply by ruthlessly removing as many spawners as possible in all cycles except 1903. A somewhat different and more palatable prospect is afforded by the existence of a series of large lakes on the upper Nechako River, which at present are inaccessible to sockeye by reason of impassable waterfalls. If fishways can be provided so as to permit salmon to enter them, it will open up new nurseries which in total area exceed Shuswap Lake and Chilko Lake together.

So as not to give a wrong impression, it should be mentioned that a number of efforts have already been made to establish new sockeye runs in severely depleted areas of the upper Fraser, with almost no success. Hence it must be regarded as a rather difficult feat. On the other hand, it is unfortunate that most of these attempts were made in Eagle River, a tributary of Shuswap Lake. In this lake the dominant cycle from Adams River will presumably make it difficult for a new run to get going in any cycle other than the dominant one, at any rate if the Adams sockeye distribute themselves throughout the whole length of the lake's extended bays. Also, eggs from downriver races of fish were used for many of these trials. Foerster ('46) tested their suitability and failed to get even one adult sockeye back to Eagle River from autumn plantings of marked Cultus Lake (downriver) fingerlings made in two years, whereas in two years when Adams River (upriver) stock was used, a small fraction did return. Unfortunately it was a *very* small fraction, so that that procedure could not be recommended for general use. Because very few of the marked fish appeared even in the commercial fishery, Foerster concluded that most of the fingerlings were waylaid somewhere between Eagle River and the ocean, and that quite probably they remained in Shuswap Lake to become non-migrating residual fish. This and similar possibilities point up the fact that a transplantation is more likely to be successful if the stock used comes from

habitats and has habits which closely resemble those needed in its new home, and also if the transfer is made in as natural a manner as possible. For example, it would be desirable to select eggs from a stream having a seasonal distribution of temperature similar to that of the stream to be stocked, and to use a run which migrated at the same time of year, and lived at about the same distance from the sea, as the former run to the area being reseeded. Attention might also be given to the initial instinctive behavior that is required of the newly-hatched fry—whether they must migrate downstream to a lake, as at Adams River; or upstream, as at Chilko Lake; or first downstream and then upstream, as in getting from Morris Creek to Harrison Lake! While exactly comparable conditions may not always be obtainable, the pronounced increase in abundance of almost all upriver sockeye stocks during the past twenty years makes it possible now to have a much wider choice of donor runs than was available formerly. If the restocking of the entire Fraser watershed took place naturally after the ice age, man need not easily despair of being able to assist in accomplishing the same thing once again.

Cycle Dominance and Lake Management

So far we have proceeded on the assumption that dominant cycles are either desirable or inevitable. Without some kind of active control by man, the second of these adjectives seems justified on the basis of present evidence. However, there is certainly a *possibility* that a greater sockeye yield could be obtained if each lake had four more or less equal cycles. This point could be determined by experiment on some small easily-controlled lake where a dominant cycle is the natural state of affairs. After a number of years of observation of its four-year yield with a dominant cycle, a switch to equality of cycles could be made by limiting the number of fish allowed to spawn in the former dominant cycle. If the result showed any pronounced difference in favor of equalized runs, it would then be time enough to give consideration to the necessary measures by which equalization could be achieved in major spawning areas.

It is interesting, however, that a kind of lake management which was proposed from quite a different viewpoint may, as an important by-product, contribute to the equalization of cycles. At Cultus Lake a campaign to reduce the abundance of piscivorous fishes was carried out in 1935–37 (Foerster and Ricker, '41).

Table II. *Estimates of the yearling crop, the average weight of the yearlings, and the percentage of non-migrants, for the years of predator control in Cultus Lake.* (Data as for table 1)

Year of spawning	No. of yearlings (*thousands*)	Average wt. of yearlings (*grams*)	Percentage of non-migratory yearlings
1934	571	8.8	12.1
1935	3161	6.0	1.9
1936	1637	7.2	0.6

The broods of sockeye affected by it increased their smolt production, per unit number of fry, to three times its former average value. This gave rise to *two successive* adult migrations in which the spawners numbered more than 70,000 fish (73,200 in 1939, 74,120 in 1940). These figures are not far from the 82,500 spawners which represented the high-water-mark of the former dominant cycle at Cultus. Further, an analysis of the effects of predator control upon the lake (Ricker and Foerster, '48) shows that these large smolt migrations were produced without undue pressure upon the lake's food supply for sockeye, because a smaller number of fry was needed to produce them and hence food competition during the summer growing season was much curtailed. As a result they consisted of much larger and faster-growing fish than did comparable migrations prior to control: yearlings of the year-classes 1935 and 1936 average 6.6 grams, whereas those of 1927 and 1931 average 2.9 grams

(tables I and II). A concomitant effect of the faster growth was a sharp decrease in the proportion of potential two-year-old migrants produced by the large migrations, namely from 22–29 per cent to 1–2 per cent. The proportion of residual sockeye produced seemed also to be much reduced, as far as observations extended (through the spring of 1938). In an indirect manner, therefore, predator removal almost eliminated the kinds of sockeye concerned in the inter-cycle competition and predation which have just been suggested as being directly involved in the initiation and maintenance of dominance, while a third possible factor—the piscivorous fish themselves—were brought directly under control!

There are a number of questions still unanswered concerning predator control —for example, whether or not predator populations can be maintained at the low levels initially achieved, and whether or not control would be economically feasible on larger lakes. However, if it does prove to have some wide applicability, its potentialities are enormous. The 73,000 or so spawners at Cultus Lake in 1939 and 1940 represent 30,000 per square mile of lake surface, which is more than is achieved, in even a single cycle, by any other lake in the river system at the present time. The runner-up is the big run to the Shuswap Lakes, which has only about 20,000 spawners per square mile, and these in one cycle only.

Another advantage of reduced lacustrine mortality is that it should make it possible to exploit sockeye populations at a much higher level of abundance. Rounsefell ('49) points out that the natural rebuilding of a sockeye cycle to the level of the old big years would be inconsistent with having a large yield for the fishery. This is because the highest levels of abundance are characterized by very inefficient reproduction and survival, so that at those levels the entire spawning population is needed merely to maintain the stock, leaving nothing over for commercial use. However the effect of predator control was precisely to increase lacustrine survival rate, so that in this way a large stock can be produced from a reduced number of spawners.

Thus, combining both of the observed benefits of predator control, one might be tempted to look forward to a day when all of the cycles could contain as many fish as did the old big years, *and* the currently-customary three-quarters of these fish could safely be diverted to tinned containers. But if it comes at all, this will come only as a result of some type of active management of the great nursery lakes. The reward for successful effort along these lines will be a sockeye pack of the order of 10 million cases annually! Production on such a scale would far surpass the best performance of the fishery's earlier years, and indeed any *possible* performance under natural conditions.

Such dazzling but uncertain prospects need not lead to any neglect of measures which will make for the best fishery which can be based upon populations regulated by the traditional boom-and-bust cycle. If the dominant cycles of the different races can be distributed fairly evenly in time, and if all potentially-important nursery lakes can be opened up and stocked, the Fraser fishery will become reasonably stable and the stream will quickly regain its early title of "the greatest salmon river in the world."

Summary

1. The sockeye salmon of the Fraser River mature principally at four years of age, and spawn only once, so that among most races there are four fairly-discrete cycles in the population. In early years the cycle of 1901 was dominant; that is, it greatly exceeded the other three cycles in abundance. The only factually-based estimate which is now possible suggests that the dominant cycle was about 65 times as numerous as the "off" cycles. Considerations of catch and fishing effort support this estimate to the extent that they indicate that it must have been *at*

least 15 times the off cycles. Using a dominant: weak ratio of only 25:1, the absolute size of the old dominant runs is estimated as 160,000,000 sockeye.

2. The dominant 1901 cycle characterized the races of sockeye bred in the large upriver nursery lakes. Only one downriver lake is known to have had a dominant cycle, and it was in the cycle year 1903. The stabilizing effect of the downriver portion of the river's population somewhat obscures the contrast between dominant and off cycles, and indicates that upriver these were in an average ratio of the order of 130:1 or more, rather than 65:1 as estimated for the population of the whole river.

3. During the years 1912–1920 the original dominant cycle disappeared as such, owing to a temporary blockade of the river and a high rate of commercial exploitation. In the Shuswap Lake area a new dominant cycle has developed during the period 1922–1942, in the cycle year 1902. This dominant cycle (Cycle I) increased about 500-fold during this time, to 2,000,000 spawners, while concurrently Cycles III and IV decreased so that they now produce less than 2,000 spawners each. Cycle II is apparently considerably larger, but is at less than one-tenth of the abundance of Cycle I.

4. Some form of interaction between cycles appears to be the only possible explanation for the occurrence of dominance. Observations on one lake indicate that the dominant cycle can affect weak ones by way of competition for food in the nursery lakes, and by way of predation upon the fry of the weak broods. This is made possible by the fact that not all of the young sockeye go to sea at the customary time, which is 1½ years after the eggs are laid. Some remain a year longer before migrating, others never migrate at all. The fraction of these two types produced is greater among large slow-growing populations than among most of the small faster-growing populations, though Cycle II fish constitute an anomalous element in such a scheme. The interaction of sockeye and the other species of fish which consume them may also play some role in dominance.

5. The former synchronization of the dominant cycles of the upriver races of sockeye seems likely to have been developed at the time that region was populated following the retreat of the last glaciation. The absence of dominance from most downriver lakes may be because their available spawning areas are small and hence the largest population they can maintain is not very great.

6. Upriver lakes other than Shuswap do not exhibit typical dominance today, but their populations have not made as great recovery toward their former abundance.

7. An eventual recurrence of the original extreme dominance of one cycle, in the river as a whole, would be undesirable because of the resulting lopsided development of fishing and packing operations. This may be forestalled by guiding the populations of the upriver races which are still in process of recuperation from the disaster of 1912–20 so that dominant cycles are spread fairly evenly among the four cycle years. There are several now-inaccessible lakes which might be opened up and worked into such a program.

8. Experiments suggest some possibility of reducing or eliminating cycle dominance by control of predatory fish populations, and also of maintaining much higher population densities and yields than are possible under natural conditions.

Appendix

Data concerning the sockeye runs at Shuswap Lake (Adams River and Little River), 1922–1946. Statements in quotation marks are from the reports of J. P. Babcock and J. A. Motherwell, published annually in the Reports of the British Columbia Fisheries Department. For recent years the estimates given in the reports of the International Pacific Salmon Fisheries Commission are also included, preceded by the letters IPSFC:

Cycle I (Cycle of 1902)

1922—"20,000 sockeye in Adams and Little Rivers; surpasses the previous 8 years." (Clemens and Clemens, 1927, quote an

estimate of 20,000 for Adams River and a *very conservative* estimate of 8,000 for Little River.)

1926—"300,000–400,000 in Adams and Little Rivers."

1930—"The number of sockeye that reached Adams and Little Rivers exceeded those spawned there in 1926."

1934—"Sockeye found in Adams River and Little River show an increase of 25 per cent over 1930."

1938—"The quantities at Adams and Little Rivers were estimated as 4 or 5 times as great as in the brood year."

1942—"Every foot of the Little River and Adams River was crowded with spawning sockeye." IPSFC: 1,967,000 in Adams River; present in large numbers in Little River.

1946—IPSFC: 1,835,000 in Adams River; 419,000 in Little River and Little Shuswap Lake.

Cycle II (Cycle of 1903)

1923—"A few hundred sockeye in tributaries of Shuswap Lake."

1927—"Approximately some 100,000 were seen spawning in Little and Adams Rivers."

1931—"The number that reached Shuswap Lake did not exceed the 100,000 estimated in 1927."

1935—"The late run to the Shuswap system . . . possibly not equalling 1931, yet very nearly so."

1939—"In Adams River spawning was considerably lighter than in 1935."

1943—"The inspecting officer estimated only 5,000 sockeye in Little River and 12,000 in Adams River." IPSFC: 10,000 in Adams River; "present" in Little River.

1947—IPSFC: 200,000 in Adams River, Little Shuswap Lake and Little River.

Cycle III (Cycle of 1904)

1924—"Thompson run very small."

1928—"Approximately 10,000 sockeye in Little River; very few in Adams River."

1932—"Not more than 2,000 in each of Little and Adams Rivers."

1936—"4,000 in Adams River, 2,000 in Little River."

1940—"In Adams River and Little River spawning was heavier than in 1936."

1944—"Sockeye seeding was disappointing." IPSFC: 1,367 sockeye in Adams River.

Cycle IV (Cycle of 1901)

1925—"15,000–20,000 sockeye in Adams River and Little River."

1929—"Approximately 10,000 spawned in Little River; few were reported in Adams River."

1933—"At Little River and Adams River there was observed an increase over 1929."

1937—"Adams River and Little River were found to contain quantities very similar to the brood year."

1941—"Only a few sockeye were found in Adams River." IPSFC: 50 sockeye in Adams River.

1945—IPSFC: 58,000 sockeye in Adams River, 6,000 in Little River; of these 98.2 per cent were age III—that is, came from the 1902 cycle—so that only 1,150 belonged to the 1901 cycle.

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A YEAR OF GROWTH FOR A SHORTLEAF PINE

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The progress of silviculture and forest management will probably be greatly accelerated when there is more basic knowledge on the physiology and chemistry of the individual tree and the components of its environment. To understand the tree as an individual may be the most important step in ultimately understanding and predicting its behavior in a stand. However, it does not necessarily follow that practical fundamental research will give direct answers to most present problems in silviculture. It is more likely that the creation of new knowledge will bring about a reformulation of present problems. In this process many of them will be simplified and some will merely disappear. This paper concerns some of the basic growth phenomena observed in an individual tree.

Recently there has been considerable interest in precise measurements of radial tree growth. Such measurements may make is possible to evaluate, in a comparatively short time, the results of various silvicultural treatments. Certain trends would become evident in a few days or weeks. During a period ranging from a few months to one or two years, it should be possible to establish fairly well the results of pruning, thinning, and soil nutrient studies.

Review of Literature

Kraus (1877) is credited with having first recognized daily reversible changes in the diameter of woody stems. He found that the diameter was usually greatest at night and least during the day throughout the growing season. MacDougal ('38) refers to Pfister as using the earliest dendrometer for measuring the minute changes in woody stems. The instrument he used in 1880 was called an auximeter and did not measure radial growth. Auximeters were used to measure circumference of the tree and consisted of a band of metal (around the tree) attached to a lever pointer.

Probably the earliest work in America on precise measurements of diameter growth was that of MacDougal ('38) in the early part of this century. Because his equipment was designed to record diameter changes rather than radial changes, it was necessarily complex. He found that soil moisture conditions, dependent on rain, determine growth. MacDougal and Shreve ('24) discovered that for Monterey pine (*Pinus radiata* D. Don) there was a negative correlation between growth and rainfall, over short periods, during the growing season, and a positive correlation between growth and annual rainfall. MacDougal ('36) established the fact that high temperatures and extended periods of sunlight had an immediate negative effect on the diameter of trees during the growing season.

Reineke ('32) devised a simpler instrument for measuring radial growth, which was later modified by Daubenmire ('45). The use of this instrument, known as the dial gage dendrometer, recently has been discussed by Brown, Rose, and Spurr ('47) and Stephens and Spurr ('47). Spurr ('47) also described dendrometer measurements of thinned and unthinned red pine. Friesner and Walden ('46) found that growth initiations for white pine (*Pinus strobus* L.) in Maine varied more than a month in the spring. Reineke ('48) relates methods and techniques of dendrometer measurements to certain limitations involved in installing this equipment.

Description of the Tree Studied

This paper presents the results of some precise measurements on the rate of radial

FIG. 1. The shortleaf pine tree studied. Photograph was taken in February, 1949.

growth of a shortleaf pine (*Pinus echinata* Mill.) over a period of one year. Measurements were started on March 21, 1939, and were terminated on that date a year later. The tree (fig. 1) selected for the study was a dominant specimen in a mixed pine-hardwood stand on the Bent Creek Experimental Forest near Asheville, North Carolina. In May 1939 this tree was 18 inches d.b.h. and 65 feet in height. Its dome-shaped crown indicated that it was approaching maturity. Ten

years later the crown had taken on the flat-topped characteristic of a mature tree, and growth of individual shoots in the crown had dropped to about three inches per year. Figure 2 shows how radial growth gradually decreased during the same ten-year period.

Growth Habits of Shortleaf Pine

The growth habits of shortleaf pine and other southern pines differ considerably from those of northern pines. In the latter species, height growth is essentially completed in the first six or seven weeks of the growing season. On the other hand, height growth of the southern pines is periodic. A tree may put forth two or more leaders during the growing season, which may last from five to eight months, depending on the latitude. The elongation of each shoot or leader requires only a few weeks. Near the end of each elongation period, buds form at the tips of the new shoots. During the following "rest" period, the succulent new growth changes color and becomes darker. At the same time, the tissue becomes tougher and the thickness of the new shoot increases. After a month or more, when these secondary changes begin to slow down, the recently formed buds begin to elongate, and growth of a new shoot starts the process all over again (weather and other factors permitting).

The Experiment

Measurements of radial growth were made by the device shown in figure 3. This device consists of an external brass frame screwed tightly to the bark of the tree and a notched steel lag screw inserted through a hole in the bark. The lag screw is screwed well into the sapwood of the tree. Effective lengths of the brass and steel parts were adjusted so that the device was self-compensating for temperature changes. Measurements of the length AB were made with micrometer calipers. Changes in this length as small as 10^{-3} millimeter could be de-

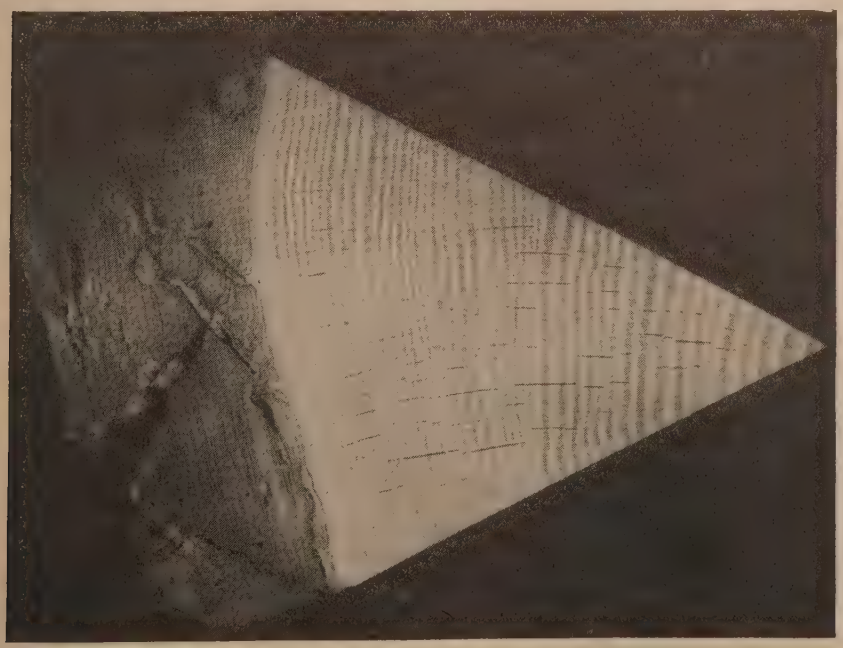

Fig. 2. Cross-section of the study tree cut in February, 1949.

tected, but it was found that daily changes were so large that measurements to 10^{-2} millimeter were sufficiently accurate. With the exception of the temperature compensation feature and the micrometer calipers, this instrument resembles the device used by Reineke and Daubermire.

With the exception of Sundays and certain days when it was not possible to make measurements, readings were taken daily at 9:00 A.M. and 4:00 P.M. during the year 1939–40. Changes in the length *AB* were interpreted as changes in the thickness of the cambium layer and neighboring tissues. Part of this change reflected actual growth, and part was a result of the divergence (both positive and negative) of water in the living tissue.

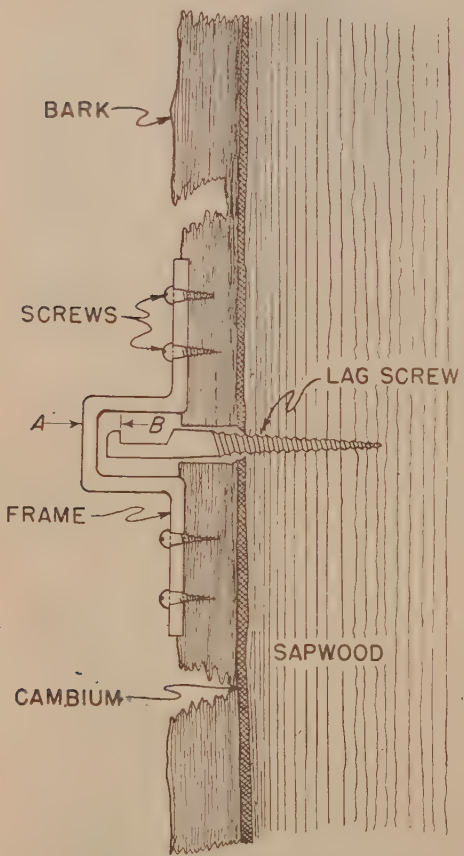

FIG. 3. Radial growth measuring device. Measurements of the distance *AB* were made periodically with a micrometer calipers.

Figure 4 shows the general trend of radial growth for a period of one year. Accumulative growth in millimeters is shown by 10-day periods. Rainfall in inches is shown for each 10-day period. It will be noticed that the average spring rate of growth is about twice as great as the average summer rate.

DISCUSSION

Figure 4 indicates that radial growth, unlike height growth, does not exhibit periodic "spurts" followed by rest periods. With the exception of minor disturbances induced by variations in conditions controlling growth, the process is continuous. It is not possible to designate specific factors as having dominant effects on tree growth. Several factors seem to share the leading role in regulating radial growth rate, and the position of most importance alternates from one factor to another.

During the spring period of rapid growth, the three most important growth factors (light, moisture, and temperature) have their optimum values, and growth is at a maximum. Figure 5 shows the growth day by day for the period from April 25 to May 25. Curves are shown for both the 9:00 A.M. and 4:00 P.M. readings. Probably none of the three factors just given had a limiting effect on growth during this period, although certain other factors such as available nutrients (nitrogen and mineral elements) and inherent characteristics of the tree may have had limiting effects. During the latter part of the period in figure 5, growth averaged about 0.025 millimeter per day. There is an average shrinkage of the cambium and neighboring tissues amounting to about 0.03 millimeter between 9:00 A.M. and 4:00 P.M., as the two curves show. Even though there is an excess of soil moisture, the tree cannot maintain a vertical transport of water equal to the transpiration rate on warm,

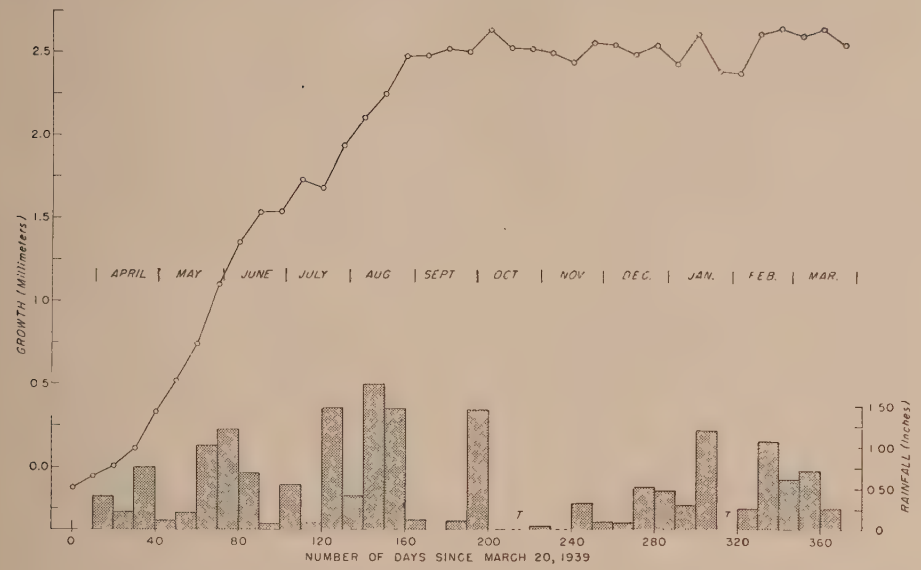

FIG. 4. Accumulative growth of the study tree by 10-day periods. Rainfall is shown for each 10-day period.

sunny days. However, the loss is temporary and is quickly made up overnight.

During June it is likely that soil moisture began to be a limiting factor in growth rate. Studies by Plice, Crafton, and Hursh ('34–'35) indicate a decline by late June in the moisture stored in the soil from winter and early spring rains. From this time on the radial growth rate averaged about one-half that of the spring period, as figure 4 shows. For the period July 9 to August 8, shown in figure 6, the limiting effect of the moisture supply on growth has become apparent. A short drought in July reversed the trend in the growth curve and, during the period this diagram covers, the daily shrinkage was about 0.06 millimeter per day,

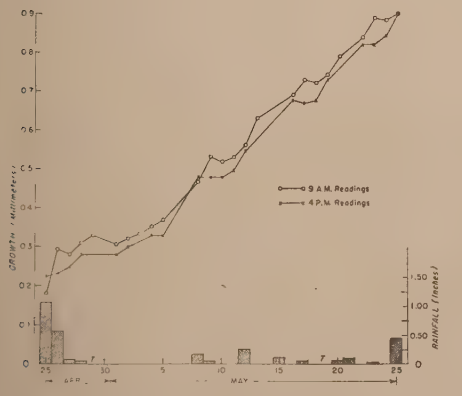

FIG. 5. Spring growth rate as related to time of reading and rainfall.

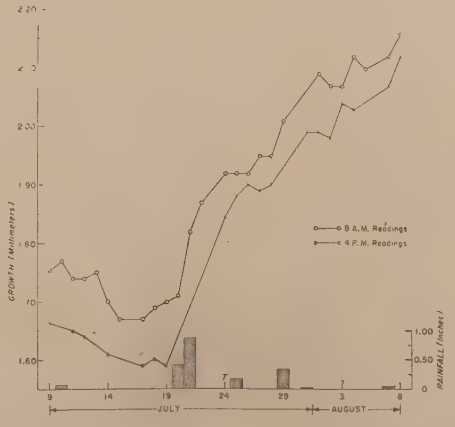

FIG. 6. Midsummer growth rate as related to time of reading and rainfall.

or more than twice that of the late spring growth period.

A reversal in the trend of the growth curve could easily be misinterpreted. Probably real growth was taking place during the drought in July, but was masked by the shrinkage resulting from continuing water loss in the outer tissues. Figure 7 illustrates the effect of a prolonged drought from October 1 to November 29. Because this drought occurred near the end of the growing season, it is doubtful that much real growth actually took place during the time that the apparent growth was negative. The length of the time for recovery following a rain seems to be determined only by the time required for the water to reach the roots.

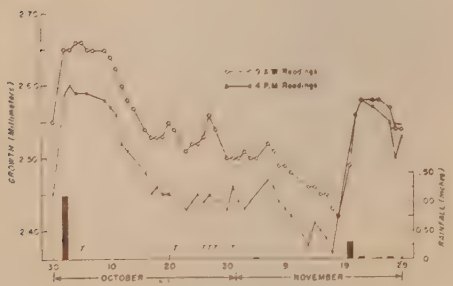

FIG. 7. Trends of growth rate during an early fall drought in 1939.

It will be noticed that rainfall has only a slight effect on growth rate during the spring, but, as the reserve moisture is used up, the growth rate becomes more and more dependent on current rainfall. It is during the latter part of the growing season that rainfall seems to be the dominant or limiting factor in growth. The total daily light absorption is also much less than earlier in the season. Before rapid growth starts in the spring, temperature and certain inherent characteristics of the tree are the limiting factors.

The general behavior of the growth curve in figures 4, 5, 6, and 7 could be anticipated from a consideration of the basic nature of plant growth. The energy of sunlight, working through the medium of chlorophyll, builds wood substance from water and carbon dioxide. For the continuation of the process, a few other variables make important contributions. The temperature must be right, and certain mineral elements and nitrogen must be available in the soil. Small quantities of some elements are also components of wood substance. The rate of the whole process can be limited by any one essential factor.

The period from January 3 to February 12 is shown in figure 8 and illustrates a phenomenon which is more difficult to explain than the behavior of the growth curves for the preceding months. This period included one severe cold spell and part of another. Rainfall has but little effect on the growth curves at this time of year because the tree is virtually dormant and ground moisture is not a limiting factor. For this reason, rainfall is not shown in figure 8 and daily air temperature[1] is given instead. If part of the moisture in the outer xylem, cambium, and phloem tissues is in the form of free water, one would expect the micrometer reading to show a definite expansion when the free water turns to ice. Just the opposite occurs. Shortly after the onset of the cold spell starting January 19, the outer layer of living tissue underwent a surprising contraction of 0.30 millimeter, or ten times the mean daily shrinkage occurring during the season of rapid spring growth. Recovery was immediate after the freezing weather ended, and there was an expansion of 0.27 millimeter in just one day, February 1. Another strange feature was the reversal of the relative positions of 9:00 A.M. and 4:00 P.M. curves. The reversal was consistent and persisted as long as the subfreezing temperature lasted.

The anomalous behavior of the growth curves during very cold weather is difficult to explain, and the interpretation is still obscure. Possibly the free water is

[1] The average of maximum and minimum temperatures recorded by the U. S. Weather Bureau at Asheville, North Carolina.

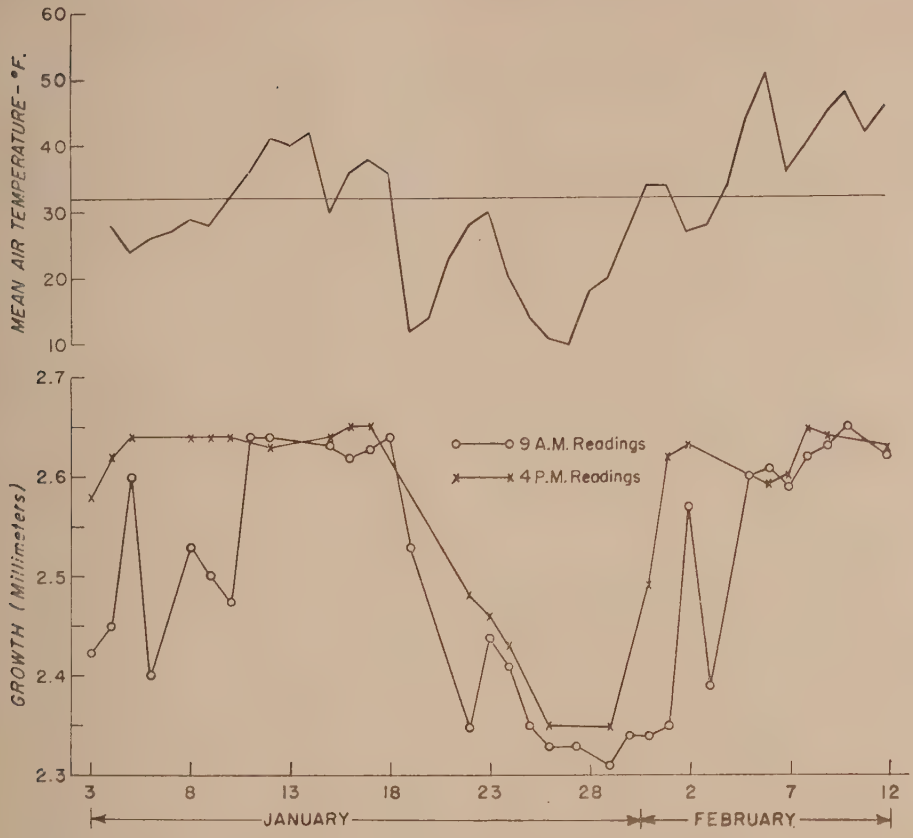

FIG. 8. Dendrometer readings for a midwinter period which includes one cold spell and part of another.

translocated to some other part of the tree. However, the contraction probably extended along the main stem and out along the branches. This would leave only the root system to accommodate the translocated water. Maybe a better explanation could be formulated around a reversible change of state in the free water. If a low temperature in some way causes the free water to change to bound water in the wood tissue, it might not be necessary to postulate a translocation mechanism. If bound water has a greater density than free water, the contraction would be a necessary consequence of the increase in density.

Another possible explanation, suggested by Dr. D. B. Lawrence, of the University of Minnesota, concerns a reduction in the ability of the roots to absorb soil water as the temperature drops, particularly at night. Continuing transpiration from the crown would then account for the sudden drop in the growth curves as well as their daytime reversal.

At the suggestion of Dr. P. J. Kramer, of Duke University, an attempt was made in February, 1949, to isolate the subfreezing effect by making measurements for a few days on a log (with ends sealed with paint) from the study tree immediately after cutting. However, the weather became warm and remained mild the rest of the winter, so as yet this test has not been successful.

Status of Precision Measurements

Precise measurements of radial or diameter growth are needed in studies designed to determine the effect of fire on tree growth. It is known that severe scorching retards both height and diameter growth. However, the effects of light scorching, as well as the effects of changes in the ground cover and surface soil, are not known. Diameter tape measurements are not reliable, especially if fire has burned away some of the bark. For silvicultural and fire studies on actual growth, the device described in this paper is more sensitive than necessary. For such work the dial gage dendrometer has sufficient accuracy. Owing to its lower sensitivity, it does not have to be temperature compensating.

For certain basic physiological studies, it might be desirable to have even more sensitive measurements of changes in the thickness of annular sections than a micrometer caliper could give. Such techniques might be of considerable value in studying translocation processes. The upper limit in precision would be attained in some type of interferometer. The design of these instruments can be made comparatively simple, yet measurements can be made to a quarter of a wavelength of visible light, or about 5 millionths of an inch. The effect of ringing, girdling, and sectioning on the transport of water and food in living tissue at different depths should become evident and measurable within a few minutes from the time of the treatment. Such techniques might be especially valuable in studies in which measurements of zonal increments were accompanied by the use of radioactive tracer elements.

Summary

From the results of a year's study of growth of a shortleaf pine, the following characteristics were noted. The greatest radial growth was made during the spring season, with daily shrinkages occurring on sunny days. This shrinkage, due to transpiration, was more than regained overnight. Soil moisture, as stored up from winter and spring rains, was somewhat depleted by early summer, and daily growth was about one-half that of the spring season. Net growth was reversed during a drought in July—real growth probably being masked by daily shrinkage. Current rainfall had only a slight effect on the spring growth rate, but had a definitely positive effect on the summer growth rate. Thus, in spring, temperature, sunshine, and certain inherent characteristics of the tree are limiting factors relative to growth. As the growing season progresses, rainfall gradually becomes the most important factor affecting growth.

During cold weather, rainfall has little effect on daily changes of the tree's diameter. However, subfreezing temperature seems to exert a pronounced effect. The tree shrinks drastically during severe cold periods, and expands rapidly again as the temperature rises above freezing. At present, there is no satisfactory explanation for this reversible reaction—only theories. Current studies may shed further light on this anomalous behavior of the growth curves in subfreezing weather.

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DIURNAL BEHAVIOR OF SOME NEOTROPICAL SPECIES OF *DROSOPHILA* [1]

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Species of *Drosophila* show little indication of diurnal rhythms in their behavior when observed in laboratory cultures. Bliss ('26) was the first to notice that adult *D. melanogaster* hatch from pupae somewhat more frequently during early morning hours than at other times. Poulson ('34) found this hatching rhythm more clearly pronounced in *D. pseudoobscura* and in *D. persimilis*. But with the sole known exception of *D. subobscura*, which does not copulate in the dark (Rendell '45, Wallace and Dobzhansky '47), species of *Drosophila* can be bred successfully in continuous light, continuous darkness, or in alternating light and dark, no difference in their activity being noticeable at different times of the day. Therefore, it was a startling finding when one of us observed, first in 1933, that California species of *Drosophila* show two peaks of diurnal activity in their natural habitats, one in the morning and the other before sunset.

A study of these diurnal rhythms in *D. pseudoobscura*, a species very common in western United States and in Mexico, has been reported by Dobzhansky and Epling ('44). On sunny days and at temperatures above 10–12° C, the flies come to bait from about half an hour before sunrise to 3–4 hours after sunrise; very few or no flies come in the middle of the day; another and usually quite sharp peak occurs beginning 1–2 hours before sunset, and the flies disappear abruptly 20–30 minutes after sunset; none come to bait during the night, and as a rule none of those which arrive during the light hours remain on the bait after dark. Other things being equal, the numbers of flies that come are much greater on warm than on cold days, and below 10–12° C none come. However, temperature does not determine the time when the flies are active, so that maxima of activity occur at diverse temperatures and humidities, depending upon weather and season. The time of activity is correlated with the time of sunrise and sunset; in summer the morning and the evening maxima are far apart, while in winter they approximate each other, but, at least in southern California, do not fuse. On a given day, the maxima are closer together in shady, and farther apart in open and sunny places. On cloudy and rainy days the flies may remain active from sunrise to sunset, so that the normal periodicity is more or less disturbed but usually does not disappear entirely.

Timoféeff-Ressovsky and Timoféeff-Ressovsky ('40) observed diurnal rhythms in *D. melanogaster, D. funebris*, and in species of the *obscura* group near Berlin. These species come to the bait in greater numbers during morning and evening hours than they do around noon. A similar periodicity has been observed by Burla (unpublished data) for several species in various localities of Switzerland, the data for *D. funebris* being most extensive. The periodicity is more pronounced on clear than on cloudy days, although even on very hot and cloudless days some *D. funebris* come to bait at all light hours.

The purpose of the present article is to report our observations on the behavior of *Drosophila* species in some localities of southern and central Brazil. Environments in which Drosophilidae live in tropical forests are obviously different from those in the temperate zones, and it is accordingly interesting to find out how

[1] Contribution No. 1 of the cooperative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical *Drosophila*.

the behavior of tropical species differs from that of their temperate zone relatives. As shown below, the diurnal behavior of Brazilian species is very plastic and depends upon the meteorological conditions of the day and the locality.

Methods

Drosophila are collected in forests of tropical Brazil by attracting them to bait of bananas with yeast. Roughly a kilogram of this bait is cast on the ground at each point where collecting is to be done. Shaded places are preferable. The space around the bait is cleared of twigs and branches that could impede the work with a collecting net. The flies attracted to the bait are caught in a cone-shaped gauze collecting net. Several sharp strokes of the net in the air above and to the sides of the bait suffice to catch most of the flies. The flies are then transferred to glass vials provided with filter paper to absorb excess moisture.

We have found it convenient to classify the flies collected on or near the field where they are captured. The flies are etherized and examined under low (× 10) or intermediate (× 30) power of a dissecting microscope. Under such conditions very closely related species can not be differentiated, and hence the data in the following tables sometimes refer to species groups. Thus, "medio-group" refers to *D. mediostriata* Duda, *D. mediopunctata* Dobzhansky and Pavan, plus some related, as yet undescribed, species. *D. willistoni* and *D. paulistorum* are included under *"willistoni,"* and the rare *D. melanogaster* is not separated from the much commoner *D. simulans*. In Brazil the number of species that are caught in a single locality during a single day of collecting often exceeds twenty. In the following tables the rarer species are not shown separately but are included in the totals.

Periodicity on clear days with variable temperatures and humidities

On October 24, bait was placed at twelve points within an area of about a kilometer square in a young second-growth wood near Mogi das Cruzes, state of São Paulo. Five of the twelve points were in a younger and more open grove on a hill slope, and seven in an older grove near a large pond. Temperature and humidity were measured in the latter neighborhood. Flies were collected ten times, from sunrise to sunset, on hours indicated in table I and figure 1. A total of 4,048 flies of at least 27 species were collected during the day, the more common species being distributed as shown in table I. The day was clear till noon, with isolated clouds in the afternoon, and a drizzle at sunset. Temperature rose and

Table I. *Numbers of individuals caught at various hours of the day, expressed in percentages of the total number of individuals of a given species of Drosophila caught during the whole day. Collection of October 24, 1948, at Mogi das Cruzes*

Species	Time of the day										Total for the day
	5.45	6.45	7.45	8.45	10.45	Noon	14.0	16.0	17.0	18.0	
simulans	3.3	17.3	15.5	8.0	4.7	2.0	2.2	5.8	22.7	18.6	1,436
medio-group	11.2	34.3	17.1	3.1	3.2	0.9	0.7	9.6	13.7	6.3	1,402
capricorni	3.9	20.3	21.3	11.6	5.8	1.9	2.6	8.7	11.1	12.8	414
willistoni	3.8	17.4	26.5	10.6	8.3	8.3	3.0	7.6	6.1	8.3	132
griseolineata	—	11.0	41.3	11.0	7.3	4.6	0.9	7.3	5.5	11.0	109
immigrans	2.3	12.7	25.3	3.4	1.1	2.3	3.4	17.2	21.8	10.4	87
bocainensis	3.8	29.2	29.2	7.6	—	—	—	6.3	12.6	11.4	79
guarani-group	16.9	32.3	8.8	3.7	2.2	—	3.7	8.8	18.4	5.2	136
bandeirantorum	20.8	28.4	20.8	3.0	1.5	—	1.5	7.5	6.0	10.4	67
calloptera-group	21.9	31.3	12.5	6.2	6.2	—	—	3.1	18.8	—	32
All species	5.1	25.5	19.0	6.3	4.2	1.9	1.7	7.9	16.6	11.8	4,048

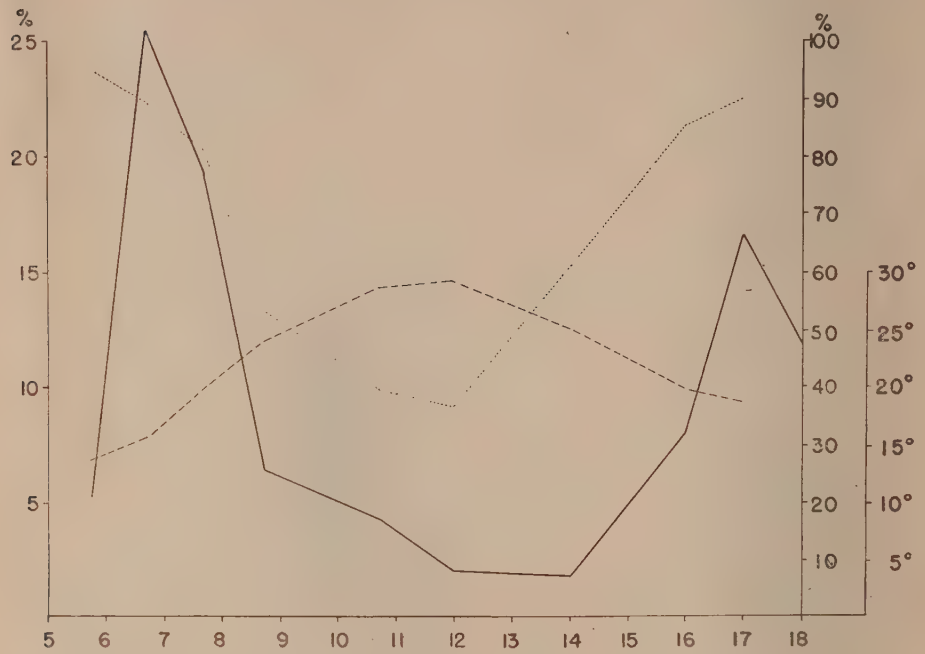

FIG. 1. Diurnal behavior of *Drosophila* on October 24 at Mogi das Cruzes. Abscissae—hours of the day. Ordinates—(on the left) percentages of the total catch of flies caught at various hours; (on the right) percentage of relative humidity, or (on the right) temperature in C°. Continuous curve—percentages of the total numbers of individuals of all species caught at different times. Dash curve—temperature. Dotted curve—relative humidity.

humidity fell sharply from sunrise till noon and a reverse change took place during the afternoon, as shown in figure 1.

It is apparent from inspection of table I, that every one of the ten species or species groups which were common enough to give meaningful data showed a clear bimodality in their activities, visiting the bait chiefly in the morning, between 6 and 8 o'clock, and again in the evening from 4:30 to 6 o'clock. Nevertheless, at no time of the day were the flies entirely absent, some coming to bait even during the hottest and driest hours of the early afternoon. A breakdown of the data shows that the bimodality was more sharp on the hill slope than near the pond (see above), but in both places some flies occurred throughout the day. It is possible, though not certain, that some species (i.e., the *medio-* and the *guarani* groups) showed a sharper bimodality than others (such as *willistoni* and *griseolineata*). These apparent differences between species should not be taken very seriously, since the collecting at the same points on the preceding day (October 23, not included in table I and fig. 1) did not give wholly consistent results so far as comparison of the behavior of different species is concerned. The observations on October 23 were, however, continued after dark, and showed that, in Brazil as well as in the United States and in Europe, *Drosophila* species do not procure food except during the hours of light and twilight.

On November 1 and 2, eight baits were exposed in a forested ravine (gallery forest) at Fazenda Monjolinho, near Anapolis, Goiaz. The weather on November 2 was of a type quite common in the tropics: clear, with rapidly rising

TABLE II. *Numbers of individuals caught at various hours of the day, expressed in percentages of the total number of individauls of a given species caught during the whole day. Collection of November 2, 1948, at Monjolinho, Goiaz*

Species	Hours of the day														Total for the day
	5.0	6.0	6.30	7.0	7.30	8.0	9.0	10.30	Noon	14.0	16.0	17.0	17.30	18.0	
nebulosa	—	11.8	14.8	15.1	16.4	12.5	7.3	3.2	4.0	6.1	3.4	2.0	1.8	1.6	1,130
bocainensis	—	14.0	11.0	18.0	17.0	8.0	3.0	3.0	—	5.0	8.0	1.0	3.0	9.0	100
polymorpha	1.3	6.6	19.8	7.9	13.2	15.8	6.6	1.3	1.3	1.3	5.3	10.5	6.6	2.6	76
simulans	—	13.2	13.2	11.5	21.3	14.8	1.6	3.3	1.6	—	4.9	4.9	4.9	4.9	61
guaramunu	—	23.1	25.0	11.6	13.5	3.8	1.9	1.9	1.9	1.9	—	5.8	9.6	—	52
willistoni	—	20.8	14.6	14.6	6.2	2.1	2.1	—	—	2.1	8.3	14.6	6.2	8.3	48
parapleta	—	8.7	8.7	19.6	6.5	6.5	2.2	—	—	6.5	6.5	13.1	15.2	6.5	46
All species	0.1	12.5	14.9	14.2	15.0	11.1	6.0	2.6	3.6	5.6	3.6	4.1	3.5	3.0	1,693

temperature and falling humidity in the forenoon, thunderheads in the afternoon, a brisk thundershower between 15 and 16 hours, and clearing toward sunset. The data on the numbers of flies collected are shown in table II, and temperature and humidity records, in figure 2. It can be seen at a glance that almost no flies were on the baits at 5 A.M. (beginning dawn), many flies appeared from 6 to 8, then the numbers of flies fell appreciably toward noon, and rose again as the cloudiness increased in the afternoon, although not to the morning height. It should be noted that the flies by no means disappeared entirely even between 10 o'clock and noon, when the humidity fell to below 50 per cent. The failure of the afternoon

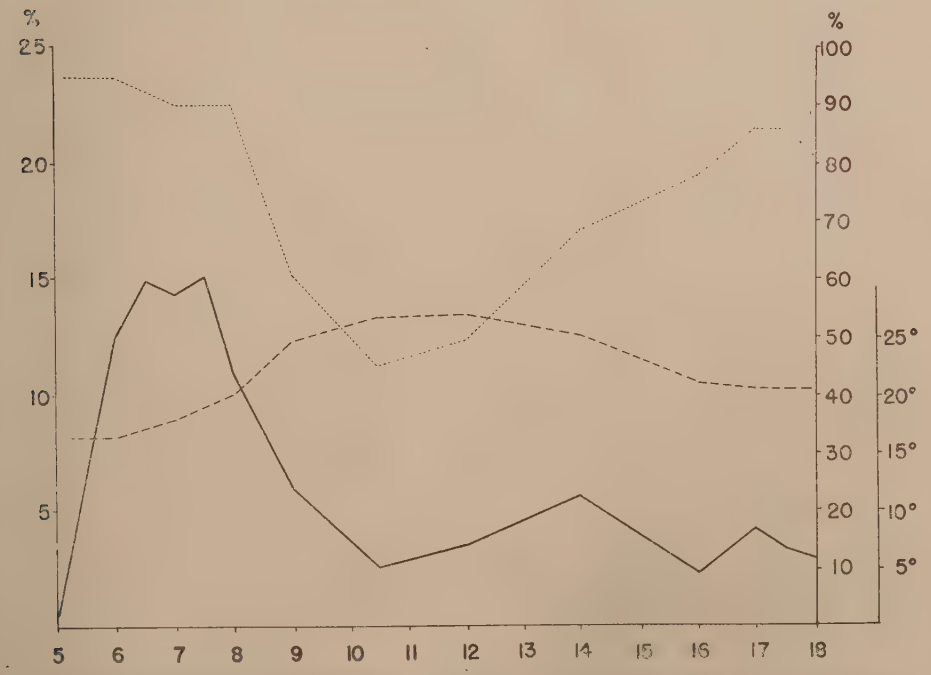

FIG. 2. Diurnal behavior of *Drosophila* on November 2, at Monjolinho, Goiaz. Abscissae and ordinates as in figure 1.

TABLE III. *Numbers of individuals caught at various hours of the day, expressed in percentages of the total number of individuals of a given species caught during the whole day. Collection of October 11, 1948, at Pirassununga, São Paulo*

Species	Hours of the day												Total for the day
	6.20	7.15	8.15	9.10	10.15	11.10	12.10	13.10	14.10	16.15	17.15	18.10	
simulans	5.3	13.5	13.9	9.9	11.5	6.1	7.7	8.8	5.7	8.3	8.1	1.0	1,617
guaramunu	3.3	3.0	6.0	6.3	5.1	7.9	7.7	13.5	6.0	16.8	18.8	5.6	430
medio-group	15.4	24.7	10.8	1.5	1.5	7.7	7.7	4.6	4.6	13.8	3.1	4.6	65
willistoni	11.8	17.7	13.7	5.9	13.7	5.9	5.9	3.9	2.0	13.7	5.9	—	51
nebulosa	—	—	4.8	9.5	14.3	9.5	4.8	23.8	14.3	4.8	14.3	—	21
All species	5.6	11.6	12.3	8.6	10.0	6.6	7.6	9.4	5.6	10.5	10.1	1.9	2,324

maximum of fly numbers to approach the level of the morning maximum may have been due in part to deterioration of the bait. However, our experience in Brazil, in contrast to that in the United States, indicates that morning maxima tend to be higher than the evening ones. The different species shown in table II behave on the whole similarly; slight differences indicated by the figures can not be regarded assured.

Behavior on cloudy and rainy days

On October 11th, bait was placed at nine points in the gallery-like forest at Baguassu, near Pirassununga, São Paulo. The day was warm, but cloudy and humid, with several brisk showers from slightly before noon till sunset. The fly collecting records and temperature and humidity data are presented in table III and figure 3. The numbers of flies increased from

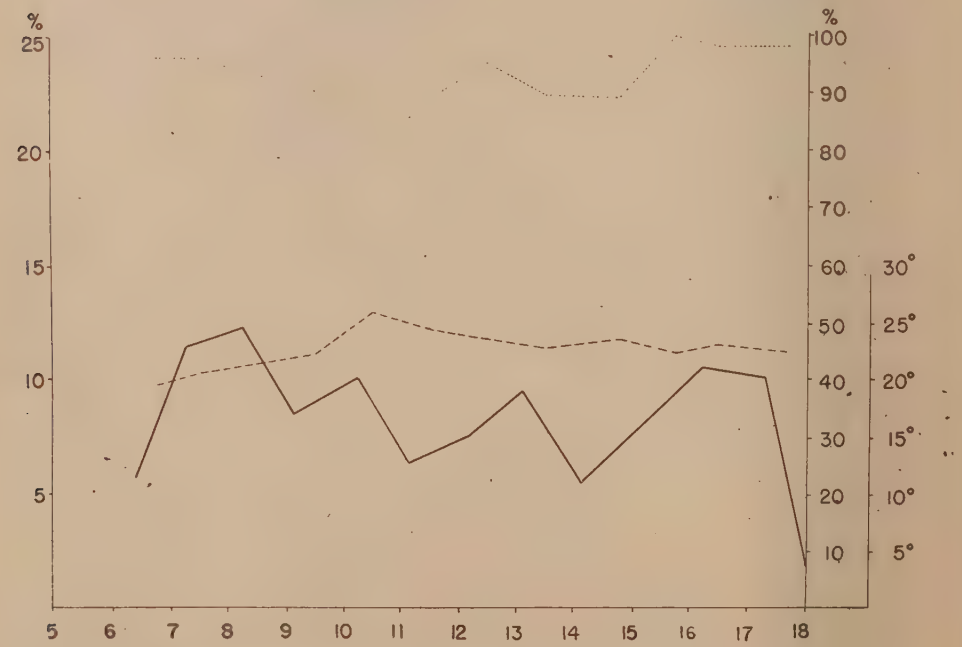

FIG. 3. Diurnal behavior of *Drosophila* on October 11, at Pirassununga, São Paulo. Abscissae and ordinates as in figure 1.

TABLE IV. *Numbers of individuals caught at various hours of the day, expressed in percentages of the total number of individuals of a given species caught during the whole day. Collection of September 26, 1948, at Vila Atlantica, São Paulo*

Species	Hours of the day								Total for the day
	6.0	8.0	9.45	11.15	13.30	15.30	16.45	18.0	
medio-group	6.6	21.3	15.5	19.1	18.4	10.6	7.3	1.2	1,081
capricorni	6.8	19.1	17.8	15.7	10.9	15.4	10.6	3.8	708
sturtevanti	1.8	16.1	15.0	17.0	11.6	19.3	13.1	6.2	648
fumipennis	11.1	28.1	21.7	11.1	10.8	10.1	5.4	1.7	406
griseolineata	1.2	7.3	5.2	18.5	25.2	12.2	11.2	9.1	385
willistoni	5.2	20.0	15.2	20.0	13.0	9.2	10.8	6.5	185
simulans	7.6	16.7	14.4	15.2	7.6	32.6	6.1	—	132
bandeirantorum	5.1	20.5	7.7	30.8	17.9	12.8	—	5.1	39
polymorpha	—	22.2	13.9	13.9	11.1	11.1	22.2	5.6	36
dreyfusii	—	20.0	40.0	16.0	12.0	4.0	4.0	4.0	25
All species	5.3	19.8	16.1	14.8	15.4	14.6	9.9	4.1	3,586

sunrise till 7 o'clock, fell slightly from 8 till noon, fluctuated irregularly during the afternoon, and fell down at sunset (the low value at 14 hours was probably due to rain that fell during the collecting). Again there were some apparent, but not necessarily significant, differences in the behavior of different species; the *medio*-group was collected chiefly in the morning, while *D. guaramunu* and *D. nebulosa* were out chiefly in the afternoon.

The collecting in the rainforest at the foot of the Serra do Mar, north of Vila

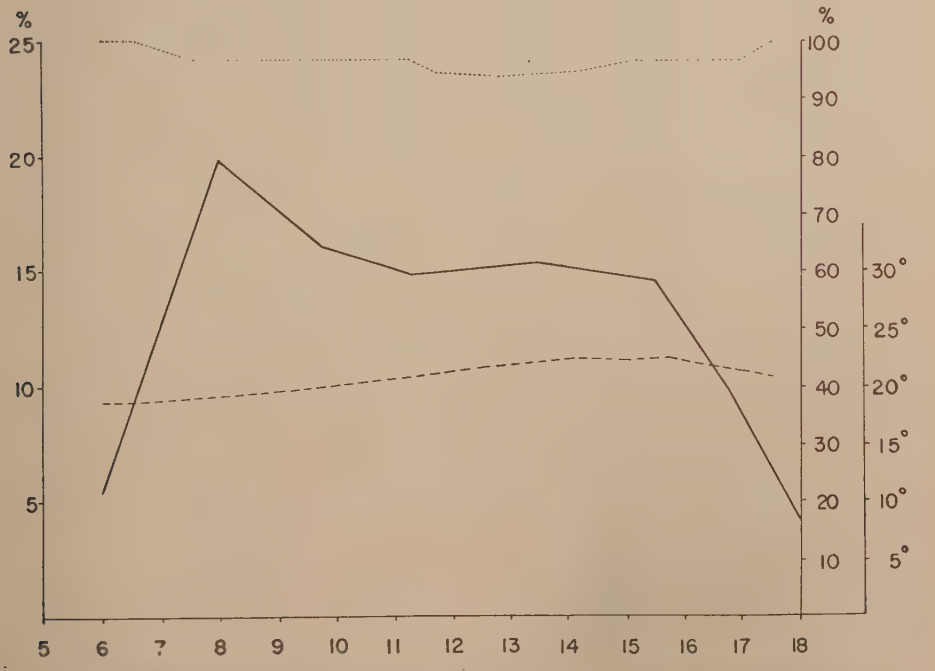

FIG. 4. Diurnal behavior of *Drosophila* on September 26, at Vila Atlantica, São Paulo, Abscissae and ordinates as in figure 1.

Atlantica, São Paulo, gave results reported in table IV and figure 4. About eight baits were placed along a trail under the forest canopy, in deep shade and permanent high humidity. The day was cloudy but rainless, with humidity approaching saturation under the canopy, and with temperature varying only from 18½° to 22½° C. Flies appeared at sunrise and disappeared at sunset. Most species (except *D. polymorpha,* of which only 36 individuals have been collected) showed no depression of numbers coming to bait during the middle of the day, and hence no bimodality in the activity curve. Whether or not such a bimodality would appear in the locality on a sunny day remains to be determined.

On January 8th and 9th, flies were collected in a "terra firme" forest near Cruzeiro do Sul, Territory of Acre. Bait was placed at about ten points in the shade of the forest and in full light on the forest margin. Sunshine alternated with cloudiness and short showers. Temperature on the forest margin varied irregularly, the amplitude being only 24°–26°, and humidity (not measured) close to saturation. No periodicity whatever was shown by the flies inside the forest, while on the forest margin the numbers of flies fell during periods of sunshine. The species involved were chiefly the *willistoni* and *medio* groups.

Discussion

Lilleland ('38) showed that, in the absence of food, *D. pseudoobscura* and *D. persimilis* die within 38–53 hours at 0 per cent relative humidity, and within 57–93 hours at 95 per cent humidity (at 24° C). Loss of water is, accordingly, a great hazard to which *Drosophila* flies are exposed in nature. They are exclusively diurnal insects, and yet the relative humidity of the air is usually lowest in the middle of the day. The diurnal periodicity of their behavior is evidently adaptive. The flies wander, procuring food chiefly or only in the morning and before sunset, when relative humidity is highest and temperature lowest during the light hours; they are inactive during the middle of the day when the danger of desiccation is greatest. Meteorological conditions are, however, not constant from day to day and in different geographic regions. In arid countries, such as southwestern United States, hot and dry days are very common. *D. pseudoobscura* and other species endemic in arid countries show striking diurnal periodicity in their behavior. Except on rainy days, the flies are wholly inactive during the middle of the day and venture abroad only in the morning and the evening.

Although this behavior is an adaptation to humidity and temperature conditions in the environment, it does not necessarily follow that it is evoked by humidity and temperature changes. Dobzhansky and Epling ('44) found their observations most consistent with the hypothesis that, in *D. pseudoobscura,* it is the light intensity which makes the flies active or quiescent (although in the morning the flies are active at higher light intensities than in the evening). Species native in wet tropics have not evolved the relatively rigid periodicity of behavior characteristic of *D. pseudoobscura.* On the contrary, Brazilian species of *Drosophila* show a remarkable plasticity. As shown in the body of this paper, on hot and dry days they are active chiefly in the morning and the evening, although some individuals continue to come to bait in the middle of the day as well. But in the humid and equable environment of the rainforests, at least on cloudy days, the bimodality disappears entirely, the flies increase in frequencies during the morning, reach a plateau during the day, and decline toward sunset. Cloudiness and rain also modify the behavior of the flies, so that the behavior patterns are quite different under different conditions. Our data do not permit the establishment of differences in behavior between different species of Brazilian *Drosophila,* although such differences are indicated by the data and their existence is inherently probable.

The nature of the stimuli that release the diurnal behavior of Brazilian *Drosophila* is also an open question; variations in relative humidity may be here more decisive than they are in *D. pseudoobscura.*

Note added in December 1949. The above conclusions have been confirmed by further observations, particularly near Belem, state of Pará, and along the lower Rio Negro, state of Amazonas, in equatorial Brazil. Little or no difference in the activity of the flies is noticeable at any daylight hour under the canopy of the Amazonian rainforest. This should be correlated with the remarkable constancy of temperature and humidity in rainforest habitats. A quite different situation was observed in September in the isolated woods ("teses") in the northeastern part of the Island of Marajó, and in July through August in the woods along the Tocantins (near Carolina and Imperatriz, state of Maranhão). Here the flies showed high morning and lower evening maxima of activity; the amplitude of diurnal changes in temperature and humidity is considerable at the time of the year stated above in these localities.

Acknowledgment

The research project of which this article is the first report has been supported by grants from the University of São Paulo, the Carnegie Institution of Washington, and the Rockefeller Foundation. The laboratory of Professor A. Dreyfus, at the University of São Paulo, served as the base of operations. Mrs. N. Dobzhansky, Dr. A. Brito da Cunha, and Prof. A. R. Cordeiro participated in the gathering of the data included in this article. The work in equatorial Brazil was made possible by the hospitality of Dr. Felisberto de Camargo, Director of the Instituto Agronomico do Norte, in Belem do Pará.

Summary

Species of *Drosophila* which are common in southern and central Brazil show a variety of diurnal behaviors correlated with weather conditions. On clear, warm, and dry days the flies are active in the morning and before sunset, and mostly quiescent during the middle of the day. In humid rainforests with equable temperatures, or on rainy days, the flies are active throughout the day. Apparently no species of Drosophila is *active* during the night. Compared to species indigenous in southwestern United States, especially *Drosophila pseudoobscura,* Brazilian species are characterized by a plasticity of behavior.

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EFFECTS OF THIRTY YEARS OF PROTECTION FROM GRAZING IN DESERT GRASSLAND

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It has long been recognized that areas protected from livestock serve as useful adjuncts in evaluating effects of grazing and in following the steps in recovery from overgrazing. Expense of fencing and loss of production usually militate against the use of large exclosures for these purposes. Small areas of an acre or two are valuable for comparison with their immediate surroundings; they do not, however, afford a variety of conditions, such as soil, slope, and aspect, and they are often severely overgrazed by rodents. Thus when the opportunity of studying a large protected area is presented, the study is well worth the time devoted to it. The information presented in this paper was gathered in a 320-acre tract of desert grassland situated about 10 miles south of Silver City, New Mexico. Except for the presence of about forty cattle for a month or two during the spring of 1948, the area has been protected from domestic livestock since 1918.

Elevation of the tract is approximately 5,600 feet. The nearest weather station is at Silver City at an elevation of 5,936 feet. Average precipitation at the station from 1878 through 1948, with some breaks before 1911, was 17.05 inches (Long, '47, '49); that from 1918 through 1948 was 16.58 inches. Of the latter average, approximately 69 per cent fell between April 1 and October 31, and 40 per cent between July 1 and September 30. Average precipitation at Deming, about 40 miles south of the study area and at an elevation of 4,331 feet, is 9.71 inches.

From 15 years of interrupted temperature records from 1911 to 1946, Long ('47) gives the average date of the last killing frost in spring at Silver City as April 25, and that of the earliest in the fall as October 24. From the same source, annual mean temperature is 53.1° F; annual mean maximum, 66.4° F; annual mean minimum, 39.8° F. July has been the warmest month, with a mean of 72.1° F; January, the coldest, with one of 35.0° F. Owing to its being 300 feet lower in elevation and 10 miles farther from the mountains, the tract under study probably experiences higher temperatures and more wind and between 14 and 15 inches of precipitation.

Soils

The soils of the area have developed on outwash material from the Burro mountains to the west. No soil survey is available for the area, but the soils appear to belong to the Whitehouse-Tucumcacori group (USDA, '38). On the upland, the surface 0–5 inch layer is a brown to dark-brown gravelly sandy loam with a friable fine granular structure and with a slightly acid reaction. This is underlain by red-brown to dark red-brown gravelly sandy loam that is somewhat heavier than the surface. The structure of this layer is coarse granular, and the reaction is slightly alkaline. Neither of the layers showed evidence of free lime when tested in the field with dilute HCl. There is approximately one per cent of organic matter in each of the layers. Below 18 inches, the subsoil is a light-brown gravelly sandy clay, slightly alkaline, and with some segragated lime. In tobosa grass flats, which are of recent alluvium, the soil is a gray-brown loam down to about 30 inches, below which it is a yellowish-brown clay loam. In table I are shown data derived from samples of the surface soils. These data indicate that there is

TABLE I. *Selected physical and chemical characteristics of the surface soil*

	pH	Total Soluble Salts	Org. Mat.	$CaCO_3$	PO_4	NO_3	K	Sand	Silt	Clay $< 2\mu$	Clay $< 5\mu$	Dispersion*
		%	%	%	ppm	ppm	ppm	%	%	%	%	%
Upland												
Outside	6.6	.04	1.2	.5	7.8	2.3	261	65.6	21.5	12.9	20.0	17.5
Inside	6.2	.02	1.0	.2	11.6	2.0	211	67.2	24.2	8.5	14.1	21.8
Lowland												
Unplowed	7.3	.04	1.7	.2	9.1	3.0	310	45.8	39.2	15.0	24.3	18.4
Plowed	7.4	.06	1.5	.2	11.2	3.4	399	45.0	40.4	14.6	24.2	15.2
Bare	7.6	.06	1.4	.1	10.9	3.4	351	45.2	41.2	13.6	23.6	16.9
Veg.	7.3	.06	1.7	.3	11.5	3.3	447	44.8	39.6	15.6	24.8	14.4

* Based on the 5-micron fraction.

little, if any, difference between upland soil in the protected area and that immediately outside.

VEGETATION

The vegetation belongs to the upper faciation of the desert grassland (Whitfield and Beutner, '38). Curly mesquite grass (*Hilaria belangeri* (Steud.) Nash), however, is wanting in this part of New Mexico.

Measurements of density of vegetation were made in June of 1946 by means of the line interception method (Canfield, '41). The lines were 100 feet long. Grasses were measured at the ground level; shrubs and half-shrubs, at the widest extent of the crown that intercepted the line. Forbs that were rooted on the line were counted. Twenty transects were measured in the protected area and six on the unprotected range outside. The outside samples were taken from upland sites contiguous to those

TABLE II. *Summary of vegetation measurements made in 1946 on protected area and adjacent unprotected upland*

	Grazed	Protected						
	Upland	Upland	Lowland*		North-facing slope	East-facing slope	South-facing slope	West-facing slope
Grasses (% cover, basal area)								
Aristida longiseta	0.23	0	0.34	0	0.73	0.42	0	0.12
Bouteloua curtipendula	0	0	0.18	0	0.28	1.64	0.08	0.70
Bouteloua eriopoda	0.24	0.16	0.98	0	0.06	0.32	0.88	1.78
Bouteloua gracilis	3.30	7.48	4.76	0.20	2.62	2.32	2.86	2.26
Bouteloua hirsuta	0	0	0	0	2.96	2.16	1.31	0.75
Hilaria mutica	0.79	0.51	0.10	3.88	0	0	0	0
Muhlenbergia torreyi	0.02	1.15	1.00	0.04	0	0	0	0
Other grasses**	0	0.34	1.40	0.70	0.07	0.04	0.29	0
Total grasses	4.58	9.64	8.76	4.82	6.72	6.90	5.42	5.61
Half-shrubs† (% cover, crown spread)	0.1	0	0	0	0.5	0.4	0.4	0.8
Shrubs†† (% cover, crown spread)	0	2.9	0.7	0.6	2.6	0.7	0.1	0
Forbs††† (number of plants per line)	0	0	0	0	4.75	3.75	0	4.00

* Two types of site: first a little higher, with sandy soil; second a tobosa grass swale, with heavy soil.

** Seven species: *Andropogon barbinodis, Aristida divaricata, A.* sp., *Muhlenbergia squarrosa, Panicum obtusum, Setaria macrostachya,* and *Sporobolus contractus.*

† Two species: *Eriogonum* sp. and *Gutierrezia sarothrae.*

†† Five species: *Echinocereus* sp., *Fallugia paradoxa, Opuntia arborescens, Prosopis juliflora* var. *glandulosa,* and *Yucca elata.*

††† Twelve species: *Artemisia* sp., *Aster hirtifolius, Astragalus humistratus, A.* sp., *Berlandiera lyrata, Circium pulchellum, Convolvulus incanus, Desmanthus cooleyi, Linum* sp., *Pentstemon* sp., *Psoralia tenuiflora,* and *Sphaeralcea* sp.

from which the upland samples on the inside were taken. Owing to the fact that no contiguous areas inside and out were available in the lowland, no lowland samples were taken outside.

Data from the samplings are presented in table II, where they have been classified according to site. Except in some of the swales, blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) was the chief dominant in the protected area and outside. In the upland samples, it constituted 78 per cent and 72 per cent, respectively, of the grass density inside and out. Total grass cover on these sites, however, was slightly more than twice as great on the inside as on the outside (figs. 1 and 2). In making such comparisons between protected and overgrazed areas, it should, of course, always be borne in mind that differences represent not alone recovery of the protected area, but the sum of this and continued deterioration outside.

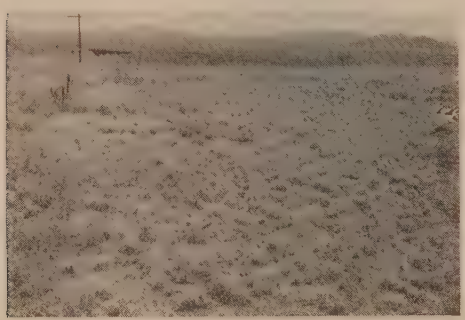

FIG. 1. View of upland vegetation protected from grazing for 28 years; June, 1946. Dominant grass: blue grama.

FIG. 2. View of unprotected range near site of figure 1; June, 1946. Dominant grass: blue grama.

Various admixtures of black grama (*Bouteloua eripoda* (Torr.) Torr.), hairy grama (*B. hirsuta* Lag.), side-oats grama (*B. curtipendula* (Michx.) Torr.), *Andropogon barbinodis* Lag., poverty three-awn (*Aristida divaricata* Humb. & Bonpl.), and other grasses appeared with the blue grama in different sites. With some exceptions, distribution of these grasses with respect to exposure was about as expected. Thus, density of hairy grama was higher on slopes facing north and east than on those facing south and west; that of back grama was higher on the slopes facing south and west. Side-oats grama, on the other hand, while having a relatively high density on the east-facing slope, had a higher one on the west-facing slope than on that facing north. Black grama, the most xeric of the four gramas, had a higher density in the lowland samples than side-oats grama. Some of these apparent anomalies may have been due to vagaries of sampling. Representatives of all these grasses could be found on the slopes outside in the protection of stones.

Tobosa grass (*Hilaria mutica* (Buckl.) Benth.) dominated a broad lowland swale that received runoff from adjacent hills and had a loam soil (tables I and II). Other lowland samples fell in a somewhat higher situation where the soil was sandy. Here, pamilla (*Yucca elata* Engelm.) formed a savannah with the dominant blue grama and black and side-oats gramas, ringgrass (*Muhlenbergia torreyi* (Kunth) Hitchc.), vine mesquite (*Panicum obtusum* H.B.K.), spike dropseed (*Sporobolus contractus* Hitchc.), and other grasses (fig. 3). Although no swales outside were sampled, observation showed that vegetation was scanty in most places, and the valleys were gutted with raw steep-sided arroyos.

Arroyos occurred on the protected

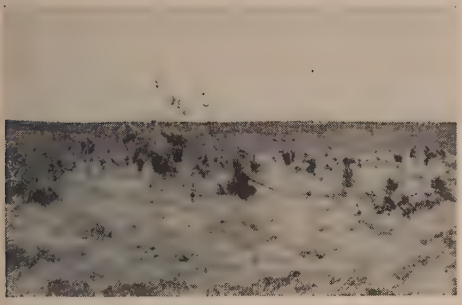

FIG. 3. View of lowland vegetation protected 28 years; June, 1946. Grasses: blue, black, and side-oats gramas, vine mesquite, dropseeds, and three-awns.

area; but in contrast to those outside they were in various stages of healing. The sides of one in the heavy recent alluvium of a swale were being overgrown by *Croton corymbulosus* Engelm. They were thus stabilized sufficiently to afford a foothold for a few plants of side-oats grama and poverty three-awn. Figure 4 shows a short arroyo leading through gravelly soil from the mesa down to the valley. In the fall of 1948, 10 species of grasses, 13 of forbs, and 2 of shrubs were observed growing in this gully. It appears, then, that, after 30 years of complete protection from livestock, these arroyos are still in process of healing and still have a long way to go.

Shrubs are not numerous on the area or immediately outside. On the upland are a few plants of mesquite (*Prosopis juliflora* var. *glandulosa* (Torr.) Cockerell) and pale lycium (*Lycium pallidum* Miers). In some of the narrow draws leading down from the upland, apacheplume (*Fallugia paradoxa* (D. Don) Endl.) occurs in considerable numbers, and a few soapberry (*Sapindus drum-*

FIG. 4. A short arroyo in gravelly soil; October, 1948. Protected since 1918. Most abundant grasses: blue and side-oats gramas.

mondii Hook. and Arn.) and hackberry (*Celtis reticulata* Torr.) bushes were observed. Pamilla is scattered over the area.

The driest year on record at Silver City was 1947, when only 6.77 inches of moisture fell. This was a deficit of 69 per cent for the year. The deficit during the growing season was 61 per cent. This was followed in 1948 by a growing season deficit of 49 per cent. In 1945 and 1946 the annual precipitation had been subnormal, with 14.40 inches and 12.55 inches, respectively; but the growing seasons had been normal. By the fall of 1948, serious loss of grass density was apparent in the protected area and on the range outside.

Six 100-foot line samples each in the protected area and on the unprotected range were taken on the upland in March, 1949, in the same general locations as those of 1946. As may be seen from table III, the drop in grass density, even allowing for sampling error, was very great—75 per cent on the inside and 78 per cent on the outside. Disproportionate loss of individual species, e.g. ringgrass, is partially, at least, due to sampling; observation failed to detect any difference between the loss of this grass and that of blue grama. Samples in the tobosa grass flat, taken in October of 1948 in the same general location as those of 1946, showed a loss of grass density in this community of approximately 50 per cent (table IV).

TABLE III. *Summary of vegetation measurements in protected and adjacent unprotected upland following severe drought. Measurements made in March 1949**

Species	Protected	Unprotected
Grasses (% cover, basal area)		
Bouteloua eriopoda	0.32	0.11
Bouteloua gracilis	1.92	.66
Hilaria mutica	.03	.19
Muhlenbergia torreyi	.04	.01
Other grasses**	.03	.05
Total grasses	2.34	1.02
Half-shrubs† (% cover, crown spread)	.1	.3
Shrubs†† (% cover, crown spread)	.3	.4
Forbs††† (number of plants per line)	.33	.17

* Measurements made in same general locations as 1946 samples, when total grass density was 9.64 per cent and 4.58 per cent, respectively, inside and outside.

** *Andropogon barbinodis, Aristida divaricata, A. longiseta,* and *Triodia pulchella.*

† *Eriogonum wrightii, Gutierrezia sarothrae.*

†† *Lycium pallidum, Yucca elata.*

††† *Astragalus* sp., *Sphaeralcea* sp.

TABLE IV. *Summary of vegetation measurements on plowed and unplowed portions of a tobosa grass flat*; October, 1948*

Species	Plowed	Unplowed
Grasses (% cover, basal area)		
Aristida arizonica	0.28	0
Bouteloua gracilis	0.80	0.16
Hilaria mutica	0	2.29
Sporobolus cryptandrus	0.21	0
Sporobolus contractus	0.04	0
Total grasses	1.33	2.45
Shrubs** (% cover, crown spread)	0	1.0
Forbs (number of plants per line)		
Chenopodium watsonni	1.8	0.6

* Plowed and cropped from 1914 to 1918, protected since.

** *Atriplex canescens, Yucca elata.*

Beginning in 1914, one end of the tobosa grass flat mentioned above was plowed and planted to crops until 1918. Since that time, it has not been touched by the plow or by grazing. Five samples each in the plowed and the unplowed portions were measured in October of 1948. The resulting data are shown in table IV, and a picture of the area appears as figure 5. Both the data and the figure show that the area has neither returned to tobosa grass nor regained a comparable cover of other grasses. Detailed observation revealed that, although there were 15 species (13 perennial and 2 annual) of grasses on the plowed area, tobosa accounted for only a trace of the cover, despite the fact that the plowed portion lies down valley from the unplowed and runoff water could be expected to carry seed from the latter to the former. The photograph shows that the line between the two portions is still sharp after 30 years.

These differences in vegetation could not be attributed to measurable soil dif-

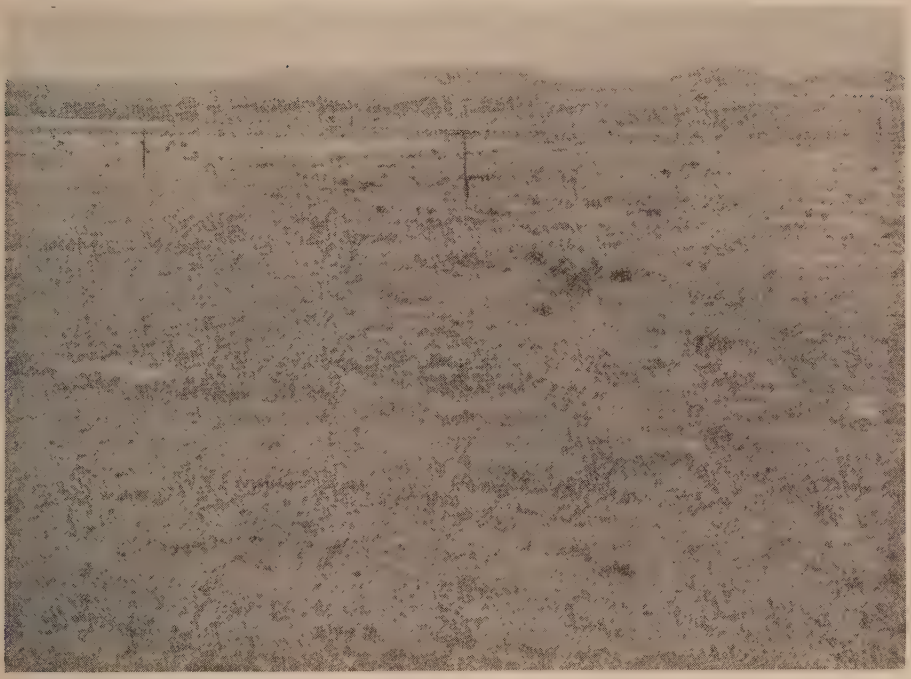

FIG. 5. View of tobosa grass flat; October, 1948. Right, plowed and cropped 1914 to 1918; left, unplowed. Both protected since 1918.

ferences. Five composite soil samples each were taken from large bare patches and large vegetated patches in the plowed portion and from the unplowed portion. Laboratory analyses of these samples showed few, if any, important differences between the soils of these sites (table I). From a statistical point of view, potassium is significantly higher in the plowed than in the unplowed area—399 ppm as compared with 310 ppm; but in neither area is it low enough to be critical. Again, potassium is significantly higher in samples from patches of vegetation in the plowed area than in those from bare patches; but the value of the latter lies between that of the former and of the unplowed area, which had a cover of vegetation. Other differences were not significant, except that for pH, which was barely so in the plowed bare portion.

SUMMARY

Observations were made on a 320-acre tract of desert grassland situated 10 miles south of Silver City, New Mexico. The area had been protected from grazing since 1918. In 1946, grass density on the upland inside the area was 110 per cent higher than that outside; there was little difference, however, in species composition between the two. Owing to lack of comparability in other types of site inside and out, such comparisons were not made on slopes and lowland.

Owing to drought in 1947 and 1948, grass density had decreased by 50 per cent on a tobosa grass flat in the area in October, 1948, and by 75 per cent on the upland both inside and out.

Gullies were raw and eroding outside; inside they were healing. After 30 years of protection, however, none was com-

pletely healed; on the other hand, none was actively eroding.

Laboratory analysis of samples of upland soil revealed no critical differences between the soil inside and that outside.

Tobosa grass had not become re-established on a flat that had been plowed and cropped from 1914 to 1918, nor had a cover of comparable density become established. Analysis of soil samples indicated that this was probably not due to soil differences attributable to plowing.

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DISTRIBUTION OF VOLUME AND RELATIVE LINEAR MEASUREMENT CHANGES IN *ACMAEA*, THE LIMPET

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Introduction

Limpets are one of the most abundant intertidal animals on rocky shores. They are distributed throughout the littoral zone both on protected and unprotected outer coasts. Since molluscan shell characteristics are particularly subject to environmental influences, differences in limpets living in these varied conditions might be expected. Russell ('07) and Orton ('32) found changes in limpet shells which they correlated with different environmental conditions. Russell found the shell of the limpet *Patella* to be lower, smaller and thicker, with a more irregular outline in exposed than in sheltered sites, while Orton found *Patella* from high water habitats to have slightly greater relative heights than those from low water habitats. The present study is an attempt to determine if similar differences occur in the common Pacific Coast genus of limpets, *Acmaea*.

Orton referred to the differences in *Patella* as changes of "shell shape." Since changes of the relation of height to width to length is what happens to produce different shell shapes, a more descriptive phrase will be used here; *relative linear masurement changes*.

The author wishes to express here his appreciation for advice and criticism offered by Dr. Irwin M. Newell in the collection and preparation of material for this study. Dr. John E. Allen and Dr. Ewart M. Baldwin are to be thanked for permission to use the map previously published by them. Dr. Ralph Mason of the State of Oregon, Department of Geology and Mineral Industries, made available the original plane table sheets for the lay-over of the map presented here.

Methods

This study was carried out on the Oregon Coast, at Sunset Bay, Lat. N.43° 20′ near Coos Bay, Oregon. Collecting was done while at the Oregon Institute of Marine Biology of the Oregon State System of Higher Education in 1947. Sunset Bay is a small coastal bay, cresentic in shape, with a constricted entrance. The North and South sides of the entrance are almost vertical sandstone outcrops, while the inner bay has a sandy shore with gravelly areas. The North side of the bay, inside the entrance, has a shelf of upended sandstone running East and West which has been fluted by differential weathering and is only visible at low tides (see fig. 1). This shelf supports a heavy growth of the alga *Laminaria Andersonii* Farlow. Very few limpets of the genus *Acmaea* occur here, *Acmaea instabilis* Gould being the only one observed. A small fresh water stream, Big Creek, empties into the South side of the bay. The North side, near the entrance, is protected by large buttress-like remnants of sandstone which protrude into the bay. A small offshore island (Squaw Island) is connected to the North end of Sunset Bay at low tides. Collecting was carried on only on the protected shore side of this island. The South side of the bay bears the brunt of the sea. The map (fig. 1) shows protecting rocks just off the South side, but even on calm days the breakers may be seen pounding high over these. Twenty-eight sites were used and a total of over five hundred specimens was collected. Specimens were collected from six sites on Squaw Island, fourteen sites on the North side of Sunset Bay and eight sites on the South side of Sun-

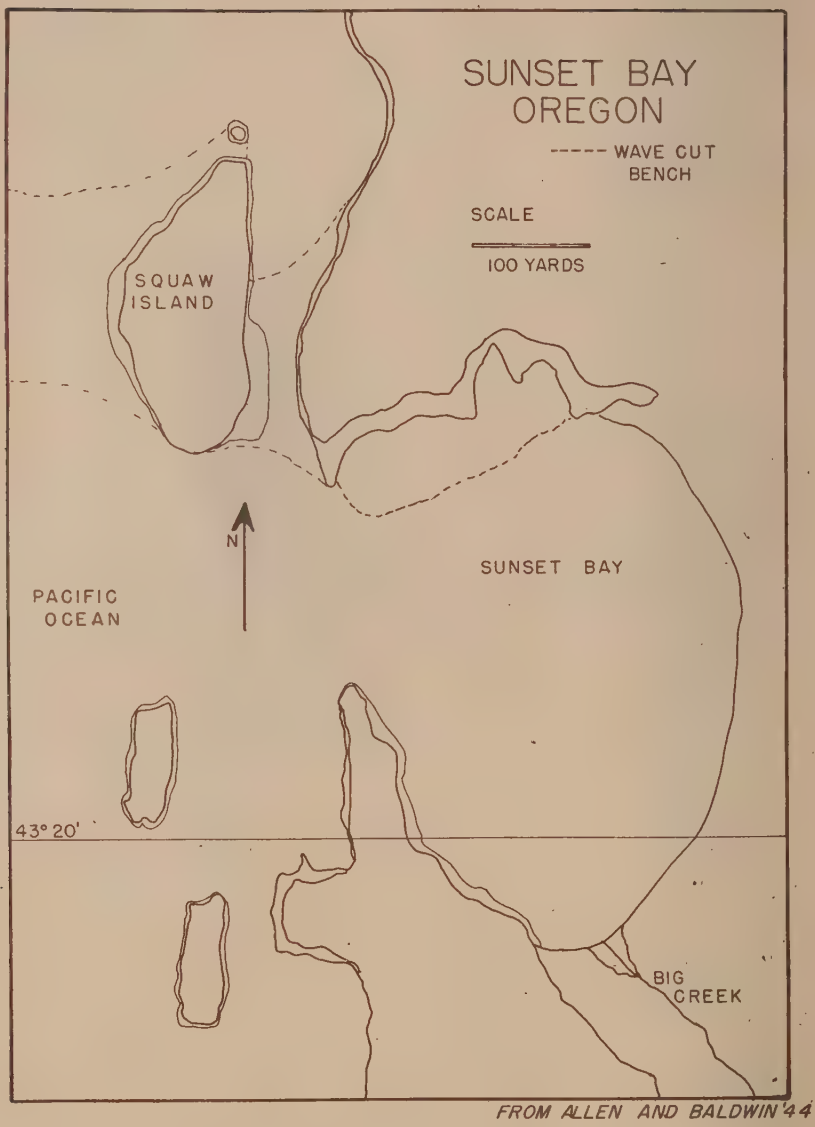


FIG. 1. Map of Sunset Bay, collecting area.

set Bay. These sites were of various heights in the tide zone from − 1.1 feet to 6 feet.

Collecting was carried on at times ranging from 6:30 A.M. to 2:30 P.M., PST, June 18, 1947 to July 2, 1947. The shells were cleaned before being measured. Measurements taken were *height, width, length* and *volume* (see fig. 2). Linear measurements were made to the nearest millimeter with calipers, while volume was measured to the nearest 0.1 cc. by using a titration burette and filling the inverted limpet shell with water. Limpets were filled until the surface of the water was exactly level with the edge of

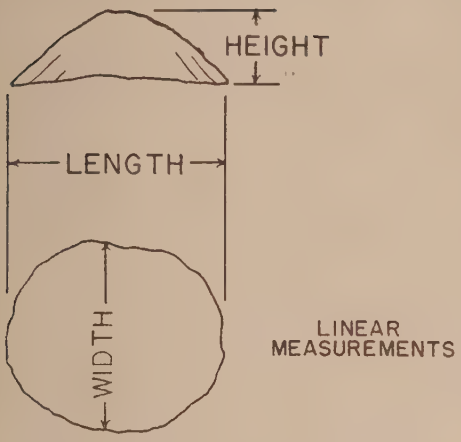


FIG. 2. Linear measurements of *Acmaea*.

the limpet. On extremely small species the method was difficult to use accurately due to surface tension effects. Therefore, volume was measured only for the larger species. The species collected and

ACMAEA SCUTUM

HEIGHT OF SITE	NUMBER OF SPECIMENS	AVERAGE VOLUME	EXTREMES OF VOLUME
-1.1 FT.	2	13.5	3 TO 24
0	10	35.8	14 - 77
0	9	30	8 - 45
0.5	12	10.5	5 - 16
0.5	7	18.7	3 - 37
1	13	82.9	7 - 205
1.5	16	9.8	2 - 18
2	1	2	——
2.5	14	30.8	4 - 59
3.5	13	9.4	3 - 22
4	7	11.1	2 - 21
4.5	3	11.3	8 - 13
4.5	1	8	——
4.5-5	32	8	1 - 19
5	6	6.1	2 - 9
5	11	5.7	1 - 13
5.5	1	3	——
6	2	6.5	6 - 7

TABLE I

ACMAEA PELTA

HEIGHT OF SITE	NUMBER OF SPECIMENS	AVERAGE VOLUME	EXTREMES OF VOLUME
0.5 FT.	4	23.5	18 TO 27
0.5	2	66.5	57 - 76
2	2	32	8 - 56
3	2	5	4 - 6
3	40	2.6	1 - 6
4	6	5	2 - 7
4.5	16	24.6	6 - 60
4.5	31	10.7	2 - 36
5	14	6	5 - 11
5	2	24	18 - 30
5.5	16	11.2	2 - 34
5.5 - 6	8	6.1	5 - 11
6	10	11.9	3 - 35

TABLE II

ACMAEA MITRA

HEIGHT OF SITE	NUMBER OF SPECIMENS	AVERAGE VOLUME	EXTREMES OF VOLUME
-1.1 FT.	5	18.4	5 TO 40
-1	14	27.1	10 - 45
-0.5	12	29.5	8 - 52
0	6	29.3	6 - 51
0	4	40.2	24 - 47
0.5	4	19.2	12 - 32
1	1	33	——
1.5	6	30.8	16 - 49
1.9	7	27	9 - 50

TABLE III

TABLES I, II, III. *Tables of height of site, number of specimens, average volume, and extremes of volume for the sites.*

the number of each is as follows:

Acmaea digitalis Eschscholtz	63
* *Acmaea scutum* Eschscholtz	141
Acmaea mitra Eschscholtz	59
Acmaea persona Eschscholtz	1
Acmaea pelta Eschscholtz	155
Acmaea asmi Middendorf	10
Acmaea spp.	35

* Probably the same species as *Acmaea testudinalis scutum* Eschscholtz (Test, A. R. (G), '45; 399).

Acmaea scutum, Acmaea mitra and *Acmaea pelta* are the only species used in this study due either to number of specimens, range in the tide zone, or general size.

Richardson ('34) found that *Acmaea persona* moves very little; Villee and Groody ('40) made similar observations for large individuals of *Acmaea scabra* and *Acmaea digitalis* and Abe (1933) in his study of limpet colonies in *Acmaea dorsuosa* Gould, reports that the movements away from the colony occur in the colder months. Abe also shows the colonies to be well formed and stable during the months the material was collected for this study. In view of these facts, it seemed unnecessary to take into account movement as a source of error.

Results

To determine if relative linear measurements occur in relation to position in the tide zone, as found by Orton, average height and width of *Acmaea* for sites were computed as per cent of average length at the same sites. These were plotted against position in the tide zone in feet above or below mean low water, zero. These are presented here as figures 3, 4, and 5. Figures 3, 4, and 5 do not show exact variations due to the reduction of length variations to a straight line, 100 per cent. This does not effect the usefulness of these figures as they are used only to show similarity of variation and not total variation. If changes relative to high or low position in the tide

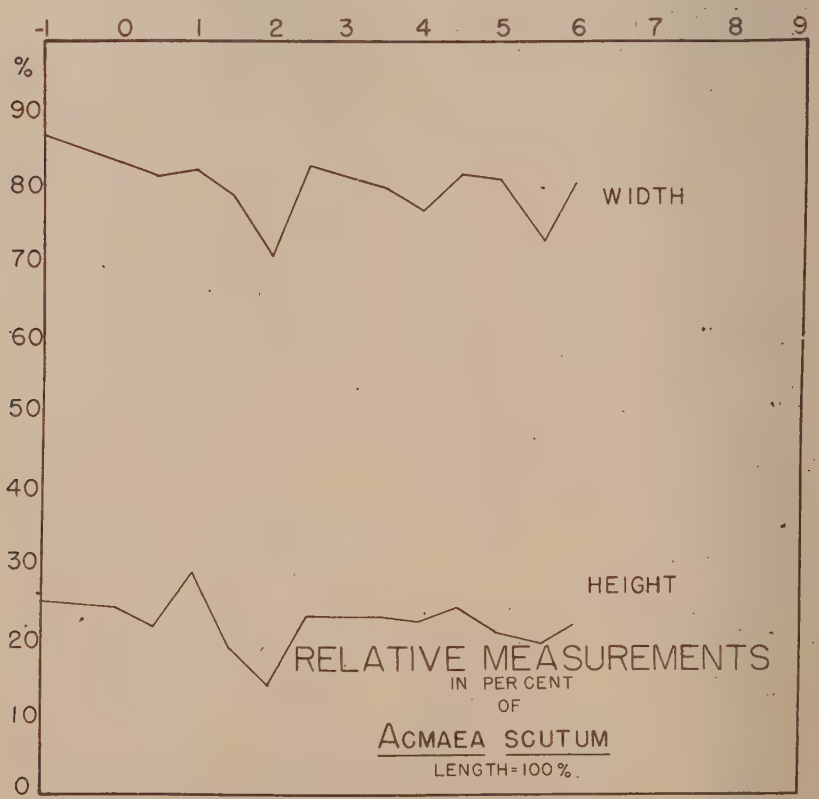


Fig. 3

zone are present, they should show in the figures above as a constant increase or decrease of percentage. Percentage changes occur but are inconsistent in direction.

Figures 6, 7, and 8 are graphs of average volume of *Acmaea* in tenths of cc in relation to position in the tide zone in feet above or below mean low water, zero. Tables I, II, and III show the position of sites in the tide zone, the number of specimens collected at each site, the average volume and extremes of volume of the specimens. These graphs and tables show the wide variations in volume of *Acmaea*. Distribution of size is also evident. The average volume may be seen to increase from upper tide zone sites to lower ones in *Acmaea scutum* and *Acmaea pelta*. *Acmaea mitra* shows no conclusive average volume changes.

It was found on comparison of figures 3 and 6, 4 and 7, and 5 and 8, that the peaks and lows of these figures occurred at the same intertidal positions. That is, average volume variations seemed to correlate with relative linear measurement variations. Such a possibility was then examined.

To compare linear measurement with volume, it was necessary to convert linear measurement to volume. This was accomplished by cubing the linear measurement to produce a volume dependent solely on the linear measurement employed. This artificial volume was then

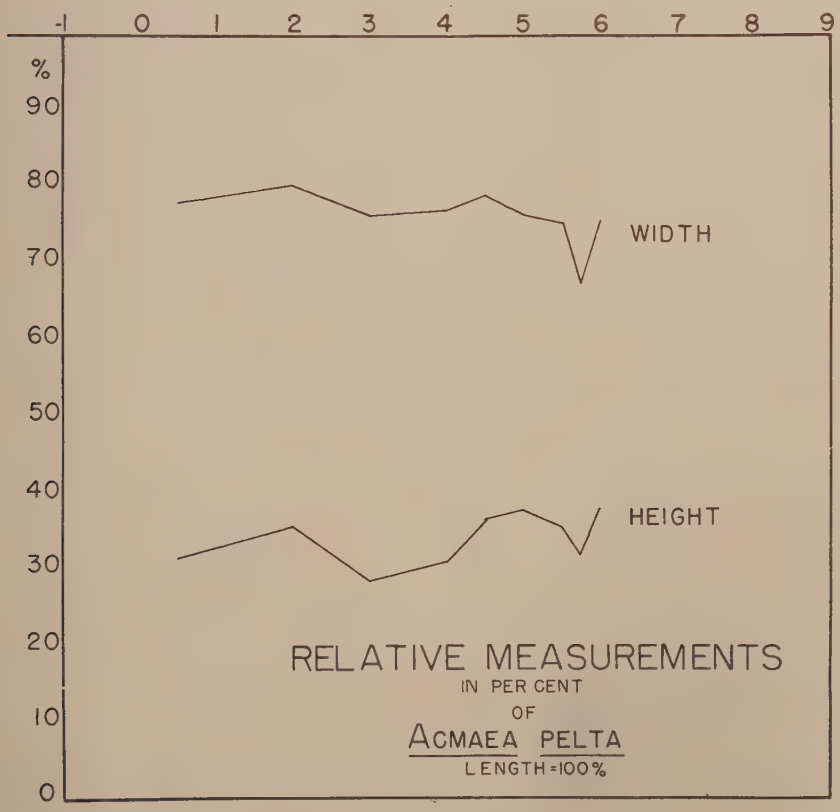
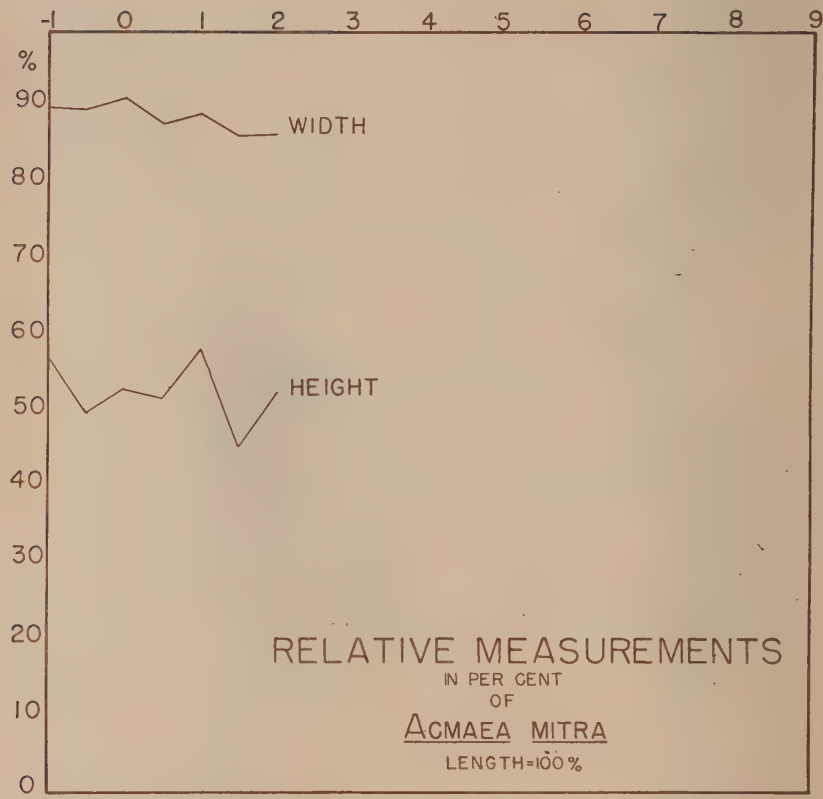


FIG. 4



FIGS. 3, 4, 5. Graphs of per cent, width and height are of length against position in the tide zone from −1.0 feet to 9.0 feet (from mean low water, zero).

divided by the actual volume to produce a ratio of volume to linear measurement. Such a ratio will show proportional changes of linear measurement when computed for a number of different volumes. These ratios were computed using height, width and length for each specimen of each species and graphed against increasing volume (see figs. 9, 10, and 11). The quantitative value of the ratio is of little significance in itself and is used here only to determine relative linear measurement changes.

DISCUSSION

It may be seen from these figures that *Acmaea scutum, Acmaea pelta,* and *Acmaea mitra* increase in relative height as volume increases, while at the same time relative length decreases. Width shows no relative changes. Variations in relative linear measurements then correlate with volume changes. Since volume is an indicator of size, volume increases may be attributed to growth.

In general, average volume is a function of position in the tide zone (figs. 6, 7, and 8). Variations in relative linear measurements are then relative to position in the tide zone only insofar as volume dictates. The relation is an indirect one.

Figures 6, 7, and 8 show larger specimens of species to be lower in the tide

zone and smaller ones higher. It may be observed though, from tables I, II, and III, that small specimens occur at all levels. Abe ('31) using *Acmaea dorsuosa* Gould found that smaller limpets possess a relatively greater supply of water in

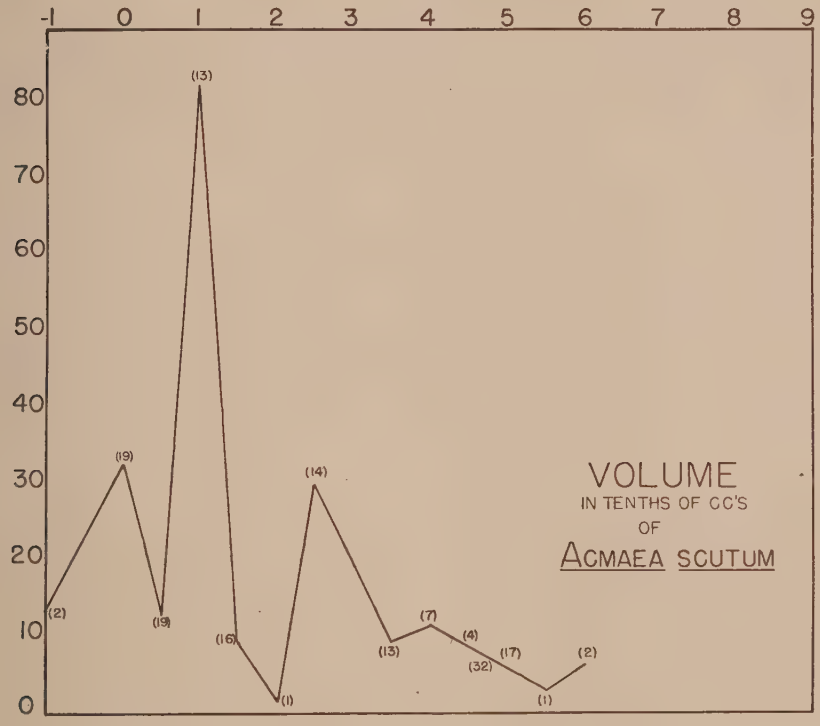


FIG. 6

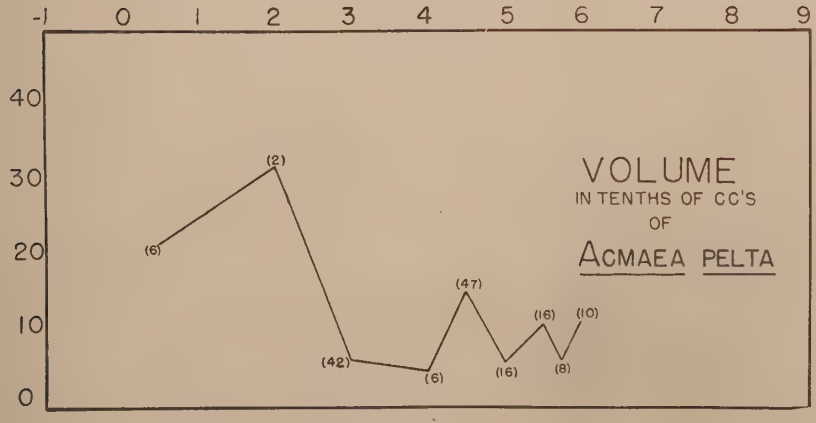


FIG. 7

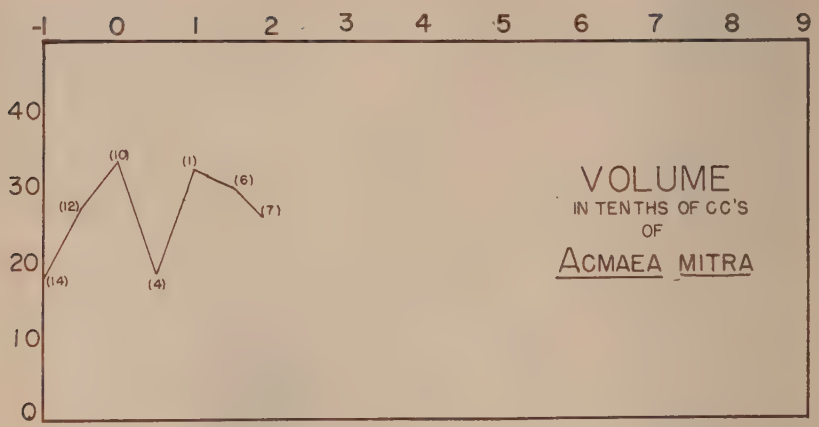


FIG. 6, 7, 8. Graphs of average volume in tenths of cubic centimeters against position in the tide zone from −1.0 feet to 9.0 feet (from mean low water, zero). Numbers in parenthesis are number of specimens from that particular position in the intertidal area. (Note similarity of occurrence of peaks and lows in figures 3 and 6, 4 and 7, and 5 and 8.)

the subnuchal cavity between the mantle and shell than that found in the larger ones. This gives the smaller limpets advantage when living in the higher reaches of the tide zone where they are uncovered and need a storage of water to avoid desiccation between tides. The fact that small limpets occur throughout the tide zone, whereas the large ones are more limited to the lower areas, may be explained in this way. The lack of variation of average volume in a more constant direction of *Acmaea mitra* (fig. 8) is then probably due to its low position in the tide zone causing little selection of volume.

The average volumes of *Acmaea mitra, Acmaea scutum, Acmaea pelta,* and *Acmaea digitalis* diminish in the order named here while these species are distributed in the tide zone from lower to higher positions in the same order. This means a probable vertical species distribution of *Acmaea* on the basis of stored water.

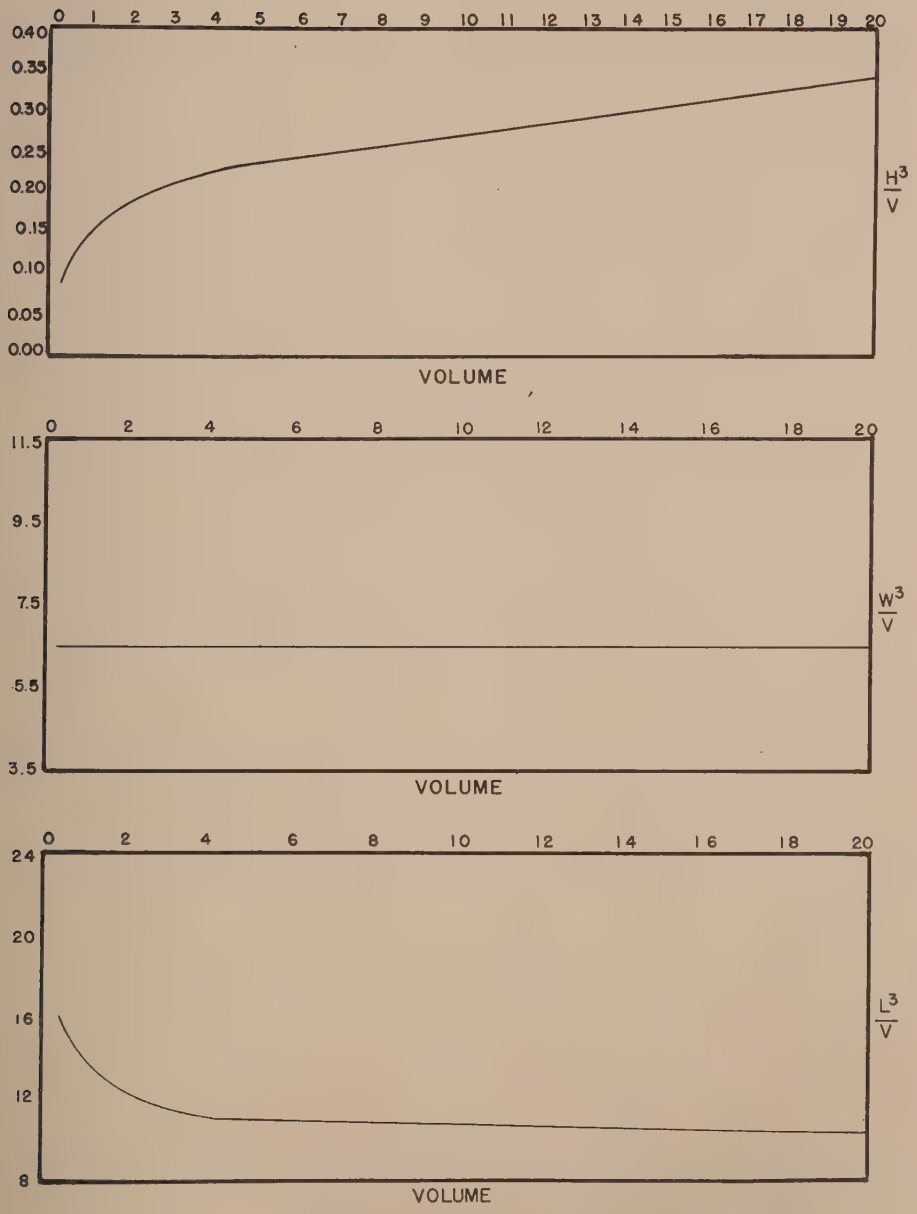
Orton's data ('32) showed *Patella vulgata* to be larger at lower habitats and smaller at higher habitats. It would seem from this that the conditions shown here for *Acmaea* are likely to be true for *Patella* also.

Acmaea, then, is distributed in relation to size and not shape, desiccation being the all important factor. This produces a vertical segregation of individuals and species. Modifications of this are to be expected since undersides of large rocks, tide pools, and other damp areas will reduce desiccation. The findings of Russell ('07) in regard to changes of size and shape may be due to modifications of this type.

CONCLUSIONS

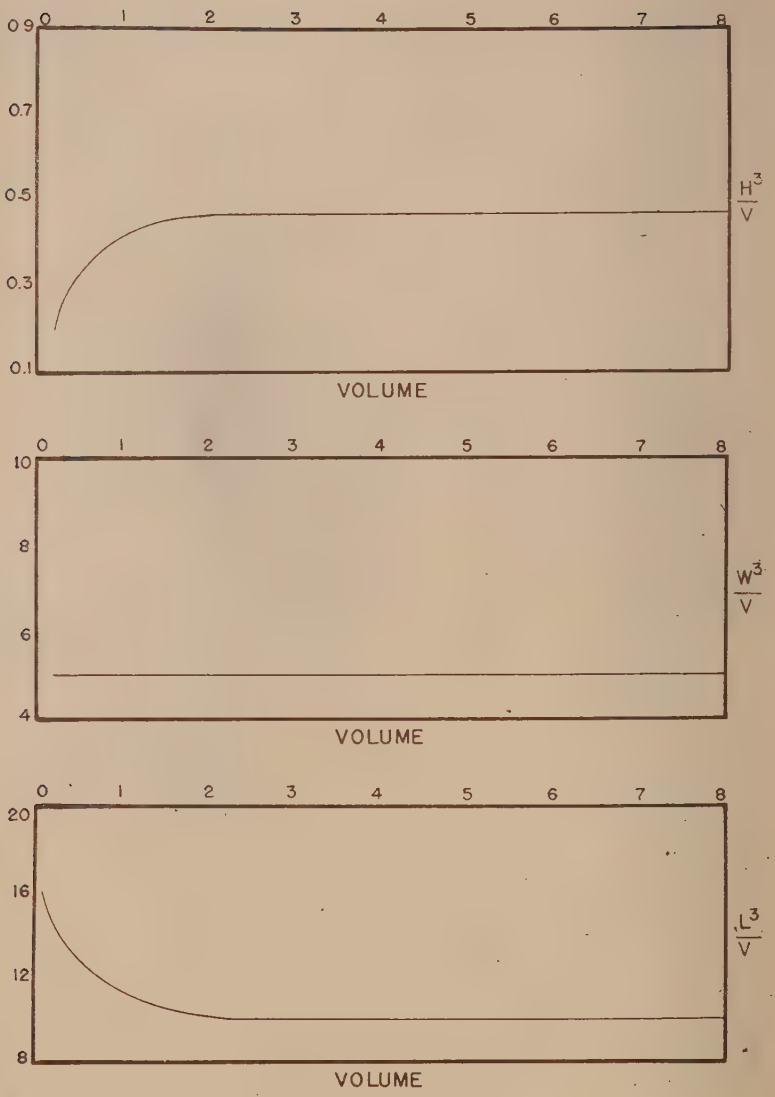
Relative linear measurement changes in *Acmaea* on the Pacific Coast of North America occur as the result of growth and not environmental differences.

The vertical distribution of *Acmaea,*



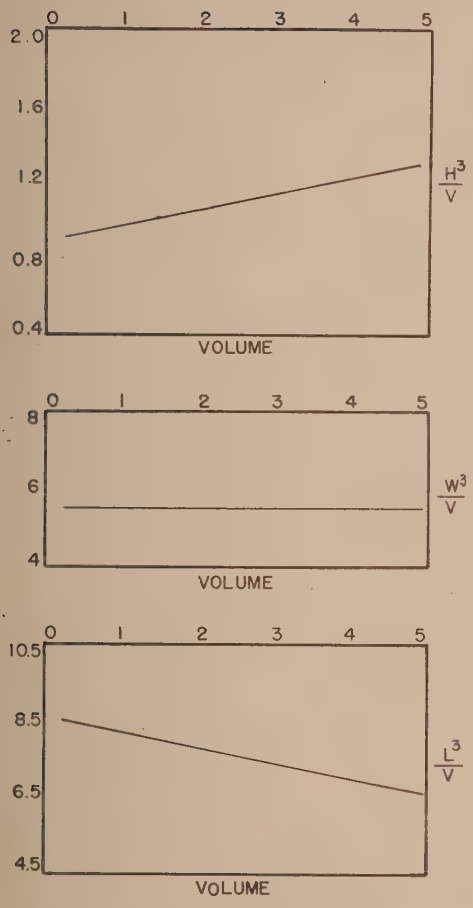
ACMAEA SCUTUM

FIG. 9



ACMAEA PELTA

Fig. 10



FIGS. 9, 10, 11. Graphs of ratios of length, width and height to volume. Volume expressed in thousands of cubic millimeters.

both individuals and species, is determined largely by resistance to desiccation. Small limpets having a relatively greater storage of water may occur higher than large ones.

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VEGETATION AND PLANT GROWTH AS AFFECTED BY CHEMICALLY ALTERED ROCKS IN THE WESTERN GREAT BASIN [1]

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Introduction

During a preliminary survey of the vegetation of the western Great Basin, numerous isolated patches of yellow pine (*Pinus ponderosa* and *P. jeffreyi*) [2] were observed in the sagebrush and pinyon-juniper zones some distance to the east of the pine forests of the Sierra Nevada. Unlike the usual postclimax extensions of forest into grassland or brush, most of these groves are on hill-sides or ridge-tops. They are remarkable also for their uniformly light yellowish soil which contrasts sharply with the brownish soils of the surrounding sagebrush or pinyon-juniper matrices.

Further investigations have revealed more than 125 of these pine stands scattered along the Virginia Range and the eastern foothills of the Sierra. The majority occur on hillsides facing the Truckee Meadows, a graben between the Carson Range and the Virginia Range, in southern Washoe County, Nevada. Outlying stands are present as far north as Long Valley, Lassen County, California, and as far south as Colorado Hill, Alpine County, California. The eastern limit seems to be set by groves at the old mining camp of Ramsey in the Virginia Range, about 25 miles east of Reno, Nevada, and by an extensive stand on the northwest side of Pah-Rah Mountain near Pyramid Lake.

Since the stands range in elevation from about 4,300 feet to over 7,000 feet and from the slopes of the Carson Range to the east side of the Virginia Range, some variation in climate is to be expected. The minimum mean annual precipitation is about 8 inches while some of the areas probably receive up to 15 inches or more per year. In contrast, the lower elevational limit of the Sierran yellow pine zone in this region occurs between the isohyets of 15 and 20 inches. The climate exhibits a dry summer–wet winter regime with a large proportion of the precipitation in the form of snow.

The present study was undertaken primarily to discover the reasons for the presence of trees on upland soils of a climatic region dominated by shrubs. Secondarily, it offered an excellent opportunity to investigate the effect of different parent materials on the structure of vegetation within a climax region.

Geology [3]

Before proceeding to a discussion of the vegetation, it is necessary to explain the geologic origin of the light-colored soils occupied by the pine. Examination has shown them to be the weathering products of chemically altered igneous rocks. The following description of the alteration will apply only to the Virginia Range, the site of many of the most typical of the isolated pine groves, and is based largely upon the work of Gianella ('36) and Calkins ('44) in the Comstock Lode district. The process was probably very similar at the other locations with slight differences in parent material or in the time of original alteration.

The Virginia Range is a large complex

[1] The research upon which this paper is based was aided, in part, by a grant from the Research Committee, University of Nevada.

[2] The nomenclature in this paper follows that of Peck ('41) insofar as the species are included by him.

[3] The author is indebted to Dr. Donald E. White of the U. S. Geological Survey and Dr. Vincent P. Gianella of the University of Nevada for invaluable assistance in the explanation of the geology of these areas, particularly in regard to the theories concerning the alteration.

fault block made up primarily of Tertiary lavas. The center of interest in this discussion is the Alta andesite of probable Miocene age, although other andesites and basalts are present. This andesite is a common parent material of the brownish soils of the pinyon-juniper and sagebrush vegetation which covers most of the range. Feldspars make up about 50 per cent of the Alta andesite with the other 50 per cent being ferromagnesian minerals, mainly hornblende, pyroxene, and chlorite. The principal feldspar is a plagioclase, labradorite, with a relatively high proportion of calcium.

During the Cenozoic period, probably in late Miocene time, great volumes of this andesite were altered by ascending hot waters. Calkins ('44) believes that this alteration at Virginia City is related to the intrusion of the Davidson diorite. The rising waters introduced sulfur which combined with iron in the rock to form pyrite. At the same time, the calcium-rich feldspars were decomposed, most of the calcium leaching away and leaving only the sodium feldspar or albite. Some of the magnesium was probably leached out at the same time with the remaining ferromagnesian minerals probably altered to chlorites.

This hydrothermal alteration probably occurred at a considerable depth below the surface. As a result of the alteration, the rock was changed to a pale green color and was charged with numerous crystals of pyrite. These altered masses, along with the unaltered rocks, have been subjected to considerable erosion in late Tertiary and Quaternary times. Gianella ('36) estimates that at least 3,000 feet have been removed.

As the hydrothermally altered rocks were exposed to weathering by erosion, the sulfur of the pyrites was oxidized to sulfuric acid. This acid, carried downward by percolating waters, caused a special type of weathering which might also be considered a secondary or cold water alteration. This weathering is taking place at present near the surface of the pyrite-containing altered rocks. It results in a leaching of most of the remaining bases, including sodium, in the sulfate form. Where percolating waters from these rocks emerge at the base of a cliff or road cut, crystals of calcium sulfate are frequently found.

The sulfuric acid weathering leaves almost nothing but the alumino-silicates which are apparently in the form of yellowish or whitish clays of the montmorillonite-beidellite series. Some of these clays may further weather into kaolinite but in most places this seems to be negligible because of the rapidity of erosion on the steep slopes. Where the action by acid is particularly intense, alumina is also leached, leaving a residue that is dominantly silica.

This secondary alteration by weathering of the pyrites may take place fairly rapidly as evidenced by the deterioration of the mine dumps around Virginia City. When the dumps are new, they consist of angular pieces of rather hard, greenish, hydrothermally altered rocks. After several decades, this rock seems to weather into a clay and the dumps become soft, mushy, and light-colored. In this stage, they are almost indistinguishable from the normally weathered outcrops of altered andesite. Gypsum crystals also appear at the bases of these dumps as evidence of the subsequent leaching of the remaining bases.

Hydrothermal alteration is still active in one place in the region, the Steamboat Springs area. Here, hot waters containing sulfur are altering granites, basalts, and andesites over an area of at least a square mile in the rift valley between the Virginia Range and the Carson Range. The whole zone of alteration around the springs is covered with yellow pines with the exception of the largest area of siliceous sinter that contains the active hot spring vents. This large island of pines is about 800 feet lower in elevation than the lower boundary of the Sierran pine zone and is separated from it by about 5 miles of sagebrush vegetation.

The substratum for the pines at Steamboat Springs is being produced by a near-surface combination of alteration and weathering. At the water table, there is an opportunity for H_2S and other gases to separate from the thermal waters. The H_2S is oxidized by atmospheric oxygen to sulfuric acid which leaches most of the bases from the bedrocks leaving an alumino-silicate residue. Where the action is intense, only SiO_2 and TiO_2 remain. Other parts of the pine-covered area are underlain by sinter deposits consisting dominantly of silica. In one place occupied by the pine and appearing very much like the old weathered altered outcrops of the Virginia Mountains, the thermal gradient is still very steep. On a cold winter day, the following soil temperatures were observed: 68° F at 10 cm, 89° F at 17 cm, 138° F at 50 cm, and 152° F at 60 cm. Such temperature phenomena are probably very local and do not seem to exist near the surface outside of the Steamboat Springs area.

Vegetation

The vegetation of the altered areas is chiefly characterized by open scrubby stands of *Pinus ponderosa* and *P. jeffreyi*. These edaphically controlled communities occur principally in the sagebrush (fig. 1) and pinyon-juniper (fig. 2) zones, but also are found embedded in the matrix of the Sierran yellow pine zone itself. All of the pine stands on altered rocks differ from those in the climatic pine zone by lacking a shrubby layer and in the paucity and distinctiveness of their herbaceous flora.

Table I presents a comparison of the structure of the arborescent flora of two pine stands on altered rocks with that of the adjacent woodland or forest on normal parent material. In the Virginia Range, *Pinus ponderosa* and *P. jeffreyi* are confined to the altered rocks while the unaltered rocks are occupied by *Pinus monophylla* (pinyon) and *Juniperus utahensis* with shrubs, grasses, and forbs cov-

Fig. 1. Isolated stand of yellow pines (*Pinus ponderosa* and *P. jeffreyi*) on altered andesite surrounded by sagebrush vegetation on unaltered andesite. Peavine Mountain foothills, about 4 miles northwest of Reno, Washoe County, Nevada.

FIG. 2. Stand of yellow pines on altered andesite (left) surrounded by pinyon-juniper vegetation (*Pinus monophylla* and *Juniperus utahensis*) on unaltered andesite. Note lack of shrubs and herbs on altered rock as compared to abundant ground cover of low shrubs, grasses, and forbs on unaltered rock at right. Geiger Grade area, Virginia Mountains, 12 miles southeast of Reno, Washoe County, Nevada.

TABLE I. *Comparison of density and basal area of trees over 1 inch d. b. h. on sites differing primarily in alteration of parent material. Data based on a sample of 1,000 square meters at each station. Density expressed as number of stems per 1,000 square meters; basal area, in square feet per 1,000 square meters.* A *indicates altered rocks;* U *unaltered rocks*

Species	Virginia Range (second-growth stands)				Carson Range (virgin stands)			
	Density		Basal area		Density		Basal area	
	A	U	A	U	A	U	A	U
Pinus ponderosa	9	—	2.748	—	14	—	10.738	—
Pinus jeffreyi	2	—	1.052	—	23	18	3.819	76.760
Pinus monophylla	—	20	—	4.626	—	—	—	—
Juniperus utahensis	—	1	—	0.174	—	—	—	—
Pinus lambertiana	—	—	—	—	2	—	0.856	—
Abies concolor	—	—	—	—	—	8	—	15.960
Juniperus occidentalis	—	—	—	—	—	8	—	9.391
Pinus contorta	—	—	—	—	—	3	—	0.725
Abies magnifica	—	—	—	—	—	2	—	0.052
Totals	11	21	3.800	4.800	39	39	15.413	102.888

ering the ground between the small trees. In the Carson Range, under Sierran conditions, the two yellow pines are found on both altered and unaltered rocks, but the stands on altered areas are stunted and clear of underbrush, definitely indicating poor site quality. Here, the total number of tree stems per unit

area is about the same on both types of rocks, but in terms of total basal area the stand on unaltered rock is almost seven times as productive as that on the altered outcrops. One tree of *Pinus ponderosa* at the very open altered rock station showed 338 rings at breast height, was 27 inches in diameter, and only 35 feet high; another showed 179 rings, was 16 inches in diameter, and 32 feet high. The timber produced on the altered areas along the east side of the Carson Range on Evans, Alum, and Hunter Creeks is of such poor quality that it was left uncut when the forests on all sides were completely cut over during the mining boom of the 1860's and 1870's. However, most of the trees on the altered patches in the sagebrush and pinyon-juniper zones are second-growth. These stands are many miles from good timber and the old pines were cut for mine timbers and fuel. Some of the original trees in these isolated stands were of fair size in view of the fact that many were growing in a climate that supports only sagebrush and grass on the normal soils. One stump of *Pinus ponderosa* on an altered area in the sagebrush zone east of Reno was 3 feet in diameter and showed well over 200 rings. A number of trees of similar size are still standing in isolated groves surrounded by sagebrush on the south side of Peavine Mountain and the northwest side of Pah-Rah Mountain.

Pinus jeffreyi is the principal pine in the climatic yellow pine zone on the east side of the Carson Range but *Pinus ponderosa* seems to be more important on the altered areas. A number of trees in the isolated groves have the appearance of being hybrids between the two. In this region, all Sierran pines of the middle elevations seem to extend farther into the dry regions of the Great Basin on altered rocks than on normal substrata. This probably is due to the absence of competition from the climatically adapted shrubby species. *Pinus lambertiana,* for example, is practically absent on the east side of the Carson Range except on the altered rocks just southwest of Reno. Here it is quite common, but is restricted to the altered substratum. There is one small tree of this species in an altered area on the south face of Peavine Mountain in the sagebrush zone northwest of Reno. *Pinus contorta* var. *murrayana* is represented by a fruiting tree on altered andesite in the Virginia Range and at least one fruiting specimen in the Peavine Mountain areas. Both *Pinus ponderosa* and *P. jeffreyi* extend to the eastern slopes of the Virginia Range on the altered rocks.[4]

Shrubs are usually absent from these isolated stands. However, a species of Amelanchier is occasionally represented by rather healthy specimens which appear to prefer the altered soils. Scattered plants of *Prunus andersonii* are found in some stands. *Pinus monophylla* and *Juniperus utahensis* are sometimes encountered on the altered rocks. However, they do poorly on these soils and are abundant and well developed on the unaltered rocks. There is some indication, nevertheless, that the pinyon and the juniper do sometimes extend down into the sagebrush zone on these soils much as do the yellow pines. Sagebrush, *Artemisia tridentata,* and its common associates are practically never found in the altered areas.

The herbaceous flora of these rocks is extremely sparse. In fact, the absence of herbaceous and shrubby cover allows erosion of the mantle to be rapid and extreme. However, the few herbaceous species which are present exhibit interesting distributional patterns. The most characteristic indicator of weathered

[4] Since this article went to press, further exploration has added *Abies concolor, Pinus monticola, Pinus albicaulis,* and *Pentstemon newberryi* to the flora of the Virginia Range. All of these Sierran species were found on altered andesites surrounded by pinyon-juniper vegetation on unaltered rocks. Of particular interest was the occurrence of the closed-cone *P. albicaulis,* the Sierran timberline species, at an elevation of only 6800 feet in a desert mountain range.

areas of alteration is *Eriogonum robustum*. It is found at almost every location and seems to be endemic on these soils. The type locality of the species is in the altered areas near the old Geiger Grade in the Virginia Mountains (Green, '85). It is closely related to *E. lobbii* of the Sierra Nevada and is considered merely a variety by some authors. It appears to be quite distinct in many ways and will be considered a separate species here. Stokes' ('36) comment that it is probably merely a form due to "superior nourishment" seems in error, particularly in view of the extremely leached rock and the sterility of the soil.

Arenaria nuttallii, Spraguea umbellata, Lewisia rediviva, Eriophyllum lanatum var. *integrifolium, Allium parvum, Festuca arida,* and *Mimulus nanus* are the principal herbaceous species which are more or less restricted to soils derived from the altered rocks in the sagebrush and pinyon-juniper zones. Several of these are not encountered again until they are found on the weathered granites of the higher Carson Range in the subalpine zone.

The ecotones between the vegetation on the altered rocks and the surrounding climatic matrix are usually quite sharp. In many places, one can easily step from one type to the other. Some of the ecotones are broader, however, particularly where altered material has washed in from above. These wider ecotones are almost always marked by the presence of *Chrysothamnus parryi* var. *nevadensis* and in many cases by mats of *Eriogonum wrightii* subsp. *subscaposum*.

Effect of Soil on Plant Growth

The extremely leached condition of the parent material, combined with steepness of slope and lack of vegetational cover, does not allow the development of a normal climatic zonal soil. The bed rock is merely covered with a weathered mantle of soil material to a depth ranging from 1 to 5 decimeters. There appear to be no horizons in this mantle and the soil can best be considered azonal. The lower part of the soil merges gradually into whitish and quite friable weathered altered andesite. Chemical weathering, as described in a previous section, has already converted the upper part of the parent material into massive chunks of clay minerals. Mechanical weathering merely breaks down these large masses into smaller fragments.

The physical properties of the soils from altered rocks, except for the wilting percentage, are not too different from those of the soils developed from unaltered rocks of the same type. Table II presents a comparison of these properties for representative samples of the two soils. All of the values are in terms of average percentages of oven-dry weight. All were determined by standard methods except the wilting percentage. The direct method of growing oats and sunflower plants in the soils until wilted was unsuccessful because the plants failed to grow normally in the soil from the altered andesite. The plants were very small, stiff, spindly, and chlorotic. Since Bouyoucos and Mick ('47) have shown that a resistance of 75,000 ohms in a buried plaster of paris absorption block

Table II. *Certain physical properties of soils developed from altered andesite compared with those of soils developed from normal unaltered andesite*

Soil	Field Capacity	Wilting percentage	Air capacity	Mechanical analysis			
				% Sand	% Silt	% Clay	Soil type
Altered andesite	32.4	19.6	7.15	44.55	26.55	28.9	clay loam
Unaltered andesite	29.3	14.2	8.7	41.6	22.2	36.2	clay

occurs approximately at the wilting percentage of most soils, the wilting percentage was determined by the use of resistance. Blocks were buried in pans of soil which was close to the field capacity. The resistance was measured as the soil slowly dried out until it reached approximately 75,000 ohms. Samples were taken from around the blocks and the moisture in them determined by oven-drying. The only significant difference between the physical properties of the two soils seems to be in the higher wilting percentage of that from altered andesite. However, this is partially compensated for by the slightly higher field capacity of the same soil. It does not seem likely that this higher wilting percentage could account for the presence of pines on the altered rock soils since, in general, pine is more typical of mesic environments.

The effect of the altered material on plant growth, as exhibited in the first attempts to determine the wilting percentage, suggested that the causes were probably chemical and due to deficiencies of certain elements, the presence of toxic elements, or to extreme hydrogen-ion concentration. Before an investigation was made of the chemical nature of the soil, however, an experiment was set up to determine whether the growth of sagebrush in the altered soil exhibited abnormalities such as had been observed with wheat, oats, and sunflower.

First and second year plants of *Artemisia tridentata* were transplanted from the field to each of three kinds of soil in one gallon metal cans. Soil A was that derived from altered andesite, soil B was derived from unaltered andesite under sagebrush, and soil C was from unaltered granite under yellow pine. Ten cans of each age class for each soil were used except in the case of soil C where only five cans of each age class were employed. All plants in a given age class were essentially the same size at the start of the experiment. Each plant was measured at the start and at periodic intervals for six months. They were watered regularly with tap water.

TABLE III. *Comparative growth of* Artemisia tridentata *in three soils at the end of six months*

Soil	Plant Age class	Average air-dry weight of tops per plant in grams	Average net height growth in centimeters
A altered andesite	1st year	0.005	mostly dead no height growth
	2nd year	0.47	1.0
B unaltered andesite	1st year	1.795	13.8
	2nd year	5.06	10.6
C unaltered granite	1st year	2.115	16.7
	2nd year	3.80	9.4

The effect of the altered rock soil on growth was apparent almost immediately. Within one month, all plants in soil A were dead, dying, or had developed a stubby, stunted condition with little or no height growth. On the other hand, almost all those in soils B and C had doubled or tripled their original height. The experiment was discontinued at the end of six months. Table III shows the average air-dry weight of tops per plant at that time. Almost all of the first year seedlings in the altered andesite were dead and those that remained alive showed no growth in the six months period. All first year seedlings in the other soils were alive and had multiplied their initial height six to eight times. The second year plants in the altered andesite were still alive at the end of the experiment but the average air-dry weight of tops was less that half a gram and the net height growth was only one centimeter. In contrast, those in soils B and C averaged 5.06 and 3.80 grams respectively and had approximately tripled their initial heights. Figure 3 illustrates typical plants from each soil near the end of the experiment.

The growth of sagebrush roots was also markedly different in the three soils. The root systems in soils B and C were ex-

FIG. 3. Comparative growth of two-year-old *Artemisia tridentata* transplants in three kinds of soil. Left to right: soil from unaltered granite, soil from unaltered andesite, and soil from altered andesite.

tensive with normally branching, slender, thread-like roots. The root systems in soil A were shallow and made up of stubby roots which were much thicker than those in the other soils.

This effect of altered rock on growth was noted also in further experiments with corn. Ten milliequivalents each of PO_4 as NaH_2PO_4 and NH_2 as urea were added to the air-dry equivalent of 1,000 grams of oven-dry soil from altered rock. Corn grown in this treated altered soil showed almost three times the yield of corn grown in untreated altered soil but only about a third of the yield produced in untreated soil from unaltered rock. Five replications of each treatment were used. Germination in the untreated altered andesite soil was particularly hampered. The young roots of the seedlings seemed to avoid penetrating the soil. Thus many of the seedlings failed to become anchored and either fell over or dried out. If the seedling survived germination, the leaves soon showed abnormal and stunted growth and in a few days many of the plants died. The young leaves were twisted together at the tips and turned wettish and brown along the margins. General chlorosis was also apparent. Some plants showed chlorotic areas between darker green veins. These symptoms are those usually associated with deficiencies of nitrogen, calcium, magnesium, and potassium.

Root effects similar to those obtained with sagebrush were noted in both corn and wheat. The roots in the soils from altered rocks were short, club-shaped, and thick. Root hair development was curtailed and almost absent. Sections of wheat roots showed that the increase in thickness was largely due to an increase in size of the cortical cells.

The indications of deficiency symptoms with corn suggested further investigation along this line. Accordingly, experiments were set up with sagebrush and tobacco using a series of nutrient solutions. These experiments were similar to those of Allard ('42). Thirteen treatments were used. Two pots of each species in soil derived from altered andesite were employed in each treatment. The treatments are listed as follows: (1) distilled water, (2) complete nutrient solution, (3) minus P, (4) minus N, (5) minus Fe, (6) minus K, (7) minus Ca, (8) minus Mg, (9) minus S, (10) minus B, (11) minus Mn, (12) minus Cu, (13) minus Zn. In addition, two kinds of checks were used for each species: soil from unaltered andesite with only distilled water added and clean quartz sand with the complete solution. The complete solution was a standard three salt solution of $MgSO_4$, $Ca(NO_3)_2$, and KH_2PO_4 with iron added as $FeCl_3$, boron as H_3BO_3, manganese as $MnCl_2$, copper as $CuCl_2$, and zinc as $ZnCl_2$. Except for the trace elements, deficiency solutions were made up by substituting equal concentrations of the sodium salt for the cations and the chloride for the anions. Trace elements were merely omitted from their respective deficiency solutions.

Seeds of *Artemisia tridentata* and tobacco (Connecticut Seed Leaf) were sown in flats of potting soil. When the seedlings were 3 to 4 weeks old, they were lifted, washed with distilled water, and

transplanted to Kodacoat-painted pots containing 1 kilo of air-dry altered andesitic soil. After watering with distilled water for 3 days, each pot was started on its particular nutrient treatment and received equal volumes of nutrient solution or distilled water at definite intervals until the end of the experiment.

At the end of 6 weeks, all sagebrush plants in altered andesitic soil were dead except those receiving the complete nutrient treatment. These were still alive but showed little apparent growth. The check plants growing in other soils were healthy and growing. The plants receiving the complete solution treatment and the checks were continued for 2 more months at which time they were all still alive. Those in the altered rock soil, however, still showed little growth even though receiving complete nutrient solution.

The experiment with tobacco was done twice. In the first trial, both types of check plants bloomed 82 days after transplanting. Unfortunately, all treatments except those in altered soil with complete solution and those in altered soil with distilled water were discontinued on this date. The tobacco plants receiving complete nutrient solution in the altered andesitic soil both eventually reached maturity and bloomed. The first plant flowered 142 days after transplanting and the second on the 173rd day after transplanting. The plants in altered rock soil which were receiving only distilled water were still alive but showed no growth when the experiment was concluded on the 173rd day.

On the second trial with tobacco, all treatments were continued until all plants which were actively growing had matured and bloomed. At the time of flowering, the plants were harvested and the oven-dry weights of the tops determined. The average weight and height for each treatment are recorded in table IV.

All treatments but minus N, minus P, and distilled water produced flowering plants, although there was some variation in the apparent health of the plants and in the time of blooming. The plants getting distilled water and one of those receiving the minus P treatment were still alive at the end of the experiment but showed no growth in the period of 273 days. The second minus P plant died a few days before the experiment was concluded. Phosphorus deficiency symptoms were apparent in these plants at all times. Only one plant receiving the minus N solution bloomed. The plant was very small and chlorotic. Its duplicate remained stunted but alive until the experiment was ended. In contrast to this, the plants receiving complete nutrient solution grew normally and flowered at an average height of 90 centimeters. Figure 4 shows a plant in altered andesitic soil which received the complete solution treatment contrasted with one of the same age which received only distilled water.

Tomato plants were also grown to maturity (fruiting) in the altered andesitic soil by adding complete nutrient solution. Similar plants with distilled water did not grow but remained stunted with

TABLE IV. *Average weights and heights of tobacco plants grown in altered andesitic soils under different nutrient treatments*

Treatment	Average height in centimeters	Average weight of tops in grams
Minus P	1.5	0.05
Minus N	16.6	0.95
Minus S	30.75	2.8
Minus Ca	75.25	12.05
Minus Mg	32.75	4.05
Minus K	61.25	9.85
Minus Fe	52.75	7.55
Minus Zn	46.25	7.35
Minus Cu	64.5	6.45
Minus Mn	57.25	7.0
Minus B	53.0	6.45
Dist. H_2O	2.75	0.075
Complete	90.0	31.8*
Unaltered—Dist. H_2O	50.5	4.65
Quartz sand—Complete	77.5	11.4

* Weight figure based on only one plant because of accidental loss of duplicate during oven-drying.

FIG. 4. Comparative growth of tobacco in soil from altered andesite. Plant on left received complete nutrient solution; height 118 centimeters. Plant on right received distilled water; height 3 centimeters.

pronounced phosphorus deficiency symptoms.

These results seem to indicate that the soils from the altered andesites are definitely lacking in available phosphorus and available nitrogen. The absence of these essential elements acts as a limiting factor which is overcome only when an adequate amount of each is added to the soil. All other elements are evidently present in the soil in available form although the quantity of some, particularly magnesium, is probably low enough to be limiting with certain native plants.

The growth of tobacco to maturity with solutions lacking certain trace elements is not to be taken as absolute evidence that all of these elements are available in sufficient quantities in the altered soil. Facilities were lacking to sufficiently purify the salts used in these experiments and small amounts of these trace metals may have been present in some cases.

As a check upon the results of the nutrient experiments, certain chemical analyses of the two types of soil were made. Standard determinations were made for total nitrogen, phosphate as P_2O_5, sulfate as SO_3, R_2O_3, and acid insoluble (mostly SiO_2). These results together with loss-on-ignition and pH determinations (with Beckman glass electrode) are shown in table V.

The total nitrogen in the unaltered soil is roughly twice the amount of that in the soil from the altered rock. However, there is a far greater difference in the amount of phosphate. The altered andesitic soil contains so little phosphate ($< 0.01\%$) that it is very difficult to detect. On the other hand, the soil from unaltered andesite shows 0.24 per cent phosphate. It may be that the real limiting factor is lack of phosphorus, as Allard ('42) found in Virginia, and that the nitrogen deficiency is the eventual result on an area too deficient in phosphorus for most plants, including legumes, to grow. The relatively poor growth of tobacco in altered andesitic soils when

TABLE V. *Certain chemical characteristics of soil derived from altered andesite compared with those of unaltered andesitic soil. Soils are those used in nutrition experiments*

Property	Altered	Unaltered
Total nitrogen	0.068%	0.177%
Phosphate as P_2O_5	<0.01%	0.24%
Sulfate as SO_3	0.46%	0.025%
Acid insoluble (mostly SiO_2)	72.485%	66.23%
R_2O_3	12.575%	13.78%
Loss-on-ignition	7.525%	8.695%
pH	4.32	7.35

not supplied with sulfate is difficult to explain in view of the much greater amount of total sulfates in these soils as compared to those soils from unaltered rocks. The poor growth may be due to a lack of easily soluble sulfates.

The two soils also differ greatly in pH. The unaltered soil supporting sagebrush vegetation has a pH of 7.35 while the altered andesitic soil shows a pH of 4.32. Further checks on soils of both types from several locations indicate that this difference is more or less constant. The altered soils generally range between pH 3.5 and 5.5 while the unaltered soils are characterized by a pH ranging from 6.5 to 7.5. This far greater acidity of the altered rocks may have much to do with the absence of sagebrush and its associates.

TABLE VI. *Base exchange conditions in soils (2 mm. mesh) derived from altered and unaltered andesites. Figures are averages of samples from three locations for each rock type*

Soil property	Altered andesite	Unaltered andesite
Total base exchange capacity (milliequivalents per 100 gms. dry soil)	24.5	33.7
Total replaceable bases (milliequivalents per 100 gms. dry soil)	3.8	30.4
Per cent base saturation	18.2	90.2
Per cent replaceable H	81.8	9.8

Since alteration of the andesite involves a leaching of the bases, the base exchange properties of the two soils were investigated. The methods used were those of Noggle and Wynd ('41). The determinations were made on soils from three different stations for each of the two kinds of soil. The figures shown in table VI are averages of all determinations.

The base exchange capacity of the soil from unaltered andesite is somewhat higher than that of the soil derived from altered andesite. The former shows an average value of 33.7 milliequivalents per 100 grams of dry soil as compared with an average of 24.5 for the latter. This may be an indication that there has been more weathering to kaolinite in the altered rock. A greater difference is shown in the total replaceable bases present. The soil from altered rock has only 3.8 milliequivalents of bases per 100 grams of dry soil while the sagebrush soil has 30.4. As a result, the soils from altered rocks show an average of only 18.2 per cent base saturation while the normal soils are 90.2 per cent saturated. This, of course, indicates a high degree of hydrogen saturation for the altered andesitic soils.

The nutrient experiments and the analyses seem to indicate that deficiencies are the principal factors in limiting the invasion of sagebrush and its associates into the areas underlain with altered rocks. However, a final experiment was set up to see if a soluble toxic substance might also be involved. Tomato plants were grown in washed quartz sand in 1-gallon glazed crocks with complete nutrient solution added at periodic intervals. Above each crock, and slightly to the side, another crock was arranged so that the drip from the drainage hole in the side of the upper crock would fall on the sand of the lower one. In one set of plants, the upper crocks were filled with soil from altered andesite; in a second set they were filled with unaltered andesitic soil, while the third set contained quartz sand as a check. Nutrient solution was added directly to the bottom crocks at periodic intervals. The upper crocks were kept filled with distilled water which filtered down through the soil and dripped as a leachate upon the quartz sand in which the tomato plants were growing. If such a leachate contained toxic elements in solution, some reduction in growth of the tomato plants could be expected. The experiment was concluded when the plants were mature and the dry weights of tops produced under the different leachates determined. There was no significant difference in the dry weights among the different treatments. Those receiving the leachate from the altered

andesite soil slightly exceeded those under quartz sand and were slightly exceeded in turn by those under soil from unaltered andesite. From these results, it seems reasonable to assume that the lack of growth in soil from altered rocks is not due to the presence of a soluble toxic substance.

Discussion and Conclusions

It has long been recognized that physical soil differences within a climatic area will result in differences in the pattern and composition of the climax vegetation. This is also true in regard to chemical differences. However, there has been less concrete evidence for the latter except for limestone soils and recent work on serpentine soils (Mason, '46; Walker, '48).

From the results of the present paper, it seems apparent that chemical differences in the form of pronounced multiple nutrient deficiencies coupled with extreme acidity produce a marked change in the vegetation within a fairly uniform climatic and vegetational area. This is not merely a change in the relative importance of the various species of shrubby dominants in the sagebrush climax, but dominance taken over completely by the tree life-form as represented by pines.

This occupation of the altered rocks by plants with a higher water requirement can best be explained in terms of compensation. *Artemisia tridentata* and its shrubby and herbaceous associates are evidently prevented from invading the areas of altered rocks by the lack of phosphorus, relative deficiencies in other elements, and acidity. These dominants of the sagebrush vegetation are better adapted climatically than the pines and their associates to the low precipitation and long drought periods. However, their absence on the altered areas allows the soil moisture of those areas to be utilized by the pines and their associated species which, in some manner, are capable of tolerating the deficiencies of the altered rocks. However, it is doubtful whether the active transpiring surface of the pines is greater than that of the same area of sagebrush vegetation since the trees are relatively small, and there is practically no shrubby and herbaceous vegetation.

The question at once arises as to why the pines and the characteristic herbaceous species are able to live on these chemically deficient soils even with available soil moisture. It may be inferred that the mineral requirements of these particular montane species are quite different from those of the sagebrush steppe plants. This is probably true and points out the need for detailed nutritional studies with important native plants. The deeply penetrating root systems of the pines in the altered rocks may compensate for some deficiencies by utilizing a greater volume of the weathered rock as a source of bases and other minerals but this could not hold for the shallowly rooted characteristic herbs. They must be adapted to low concentrations of certain elements. It is interesting to note that almost all of these same herbaceous species are characteristic of the sterile decomposed granites of the higher elevations of the Sierra.

The origin of the isolated pine patches is also of interest. The presence of these stands, containing the characteristic high montane herbs, at some distance away from the Sierra almost precludes the possibility that these areas are advance disjuncts from the montane vegetation. It seems more likely that they are relicts from a moister period when pine forests may have covered much of the Virginia Range. Even under those conditions, the altered areas would have been distinguishable from the surrounding forest as poor sites. As the climate became drier, sagebrush and its associates invaded under the pines on normal soils and by their competition for water and light prevented adequate pine reproduction. Thus, eventually, all such pine forest was replaced by sagebrush or pinyon-juniper vegetation except on the altered areas where deficiencies and acidity prevented

invasion by the shrubs and grasses. Here the pines and indicator herbs have held on in an area climatically too dry for them because of the lack of competition from sagebrush and its associates.

Summary

Pinus ponderosa, P. jeffreyi, and certain montane herbaceous plants were found growing some distance to the east of the Sierra Nevada in the semi-arid sagebrush or pinyon-juniper zones. In every case, these stands were confined to volcanic rocks which had been hydrothermally altered with resultant accelerated chemical weathering. Sagebrush and its associates will not normally grow in soils developed from the altered rocks.

Analyses show that these soils are quite acid and very deficient in exchangeable bases, phosphorus, and nitrogen as compared to soils developed from unaltered rocks of the same type. Tobacco and tomato plants did not grow in the soil when given only distilled water or nutrient solutions lacking in phosphorus or nitrogen but matured and flowered when these elements were added. It is concluded that the pine stands are relicts which have remained because of the inability of sagebrush zone dominants to invade these mineral-deficient soils.

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EVAPORATIVE WATER LOSS IN DESERT RODENTS IN THEIR NATURAL HABITAT

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Introduction

In a previous paper (Schmidt-Nielsen, '48a) it was reported that desert rodents of the family Heteromyidae can live enentirely without drinking water.

The two main paths of water expenditure in these animals are urine formation and evaporation from the lungs. These losses are covered by the water content of the food, which is very low, and by the water formed by metabolism.

It was previously reported that the animals can conserve water by excreting an extremely concentrated urine, twice as concentrated as sea water (Schmidt-Nielsen, '48b) with respect to electrolytes. The other important water loss, the evaporation from the lungs, depends upon the ventilation of the lungs and is greatly affected by the humidity of the inspired air. The higher the water content is in the inspired air, the less water is expended to bring the expired air to saturation.

Since evaporation from the lungs is a critical factor in the water balance of the heteromyids, an ecological investigation of their habitat was needed in order to furnish information as to the microclimatic factors within and outside the burrows. This ecological study was made specifically to obtain the necessary background for evaluating the physiological relations between the animals and their environment, and was not intended as a comprehensive survey of their ecological habitat.

Plan

We wished to determine the microclimatic conditions during the driest part of the year, because the figures obtained would indicate the greatest stress on the animals and give a foundation for an approximate calculation of the evaporative water loss when the environmental factors are most disadvantageous to the animal.

The late spring and early summer is the driest and hottest time of the year in the Arizona desert where our investigations were carried out. Our observations were made on the Santa Rita Experimental Range, 35 miles south of Tucson, Arizona. In this area Vorhies ('45) had made excellent recordings of the temperature in and outside the burrow of a *Dipodomys spectabilis* (bannertailed kangaroo rat) during a whole year. Outside the den he also recorded the humidity but, lacking a suitable hygrometer, he was unable to record the humidity inside the burrows. He found that the temperature in the nest chamber shows almost no diurnal fluctuations. During the summer months the temperature in the nest chamber is just below 30° C (85° F) and in the coolest time of the winter it goes down to 8° C (46° F).

We made our measurements during May and June 1948. There had been only one rainfall (18 March, 9 mm) in the area since the winter rain period ended in February the same year. We had one rainfall (4 mm) during the two month period we worked on the burrow humidity. The rainfall occurred on 6 June; it had a marked influence upon the air humidity for a few days.

Apparatus

For the measurements in the burrows, we used Krogh's microclimate recorders (Krogh, '40). The recorder is of the size of an ordinary wrist watch. It records temperature and relative humidity continuously for 12 hours. The record is made on a smoked circular glass

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disc which can be read under the microscope. The humidity sensitive element in the recorder is a hair hygrometer. It therefore has the same limitations as other hair hygrometers, i.e., it will not record relative humidity below 20% with much accuracy. After a hair has been exposed to very dry air for some time, it also takes several hours to restore its hygroscopic properties when transferred to a more humid environment.

For the outside air humidity, we mainly used ordinary sling psychrometers.

Electric hygrometers (Dunmore, '39) are very useful for a quick estimate of the humidity and temperature in an airspace too small for a sling psychrometer. A continuous record can also be made with the Dunmore hygrometer, but it requires elaborate instrumentation. We used the Dunmore electric hygrometer (Dunmore, '39) for humidity and temperature measurements in small airspaces when the humidity was too low for the microclimate recorders, and whenever a fast reading was desired. The relative humidity is determined from the resistance in a hygroscopic film of lithium chloride, the instrument is temperature sensitive and the simultaneous temperature must be known and the relative humidity is then found from calibration curves. The temperature is measured with a small resistance thermometer built into the humidity sensitive element. (The apparatus was used as supplied by American Instrument Co., Silver Spring, Maryland.)

The Krogh microclimate recorders were more useful for our field work, both because of their small size and their convenience in use. In the beginning we did not believe that Krogh's recorders would be very useful for measuring the humidities in the burrows of the heteromyids because we expected to find relative humidities lower than 20% inside the burrows. A brief survey, however, showed that the humidity in the ground and in the burrows ranged much higher than we expected. The recorders, therefore, turned out to be extremely useful for the work.

Measuring Technique

When measuring the humidity and temperature in the burrows, the following technique was used:

The animal was trapped in a live trap in front of its burrow during the night. Next morning the animal was taken out of the trap and a microclimate recorder was tied to its tail with a piece of string. To protect the recorder from dust and dirt, a piece of cloth was tied around it. In order to prevent the animal from running away with the instrument, a long, soft wire was tied to the recorder with the other end fastened outside the den. The animal was released right in front of its own den. It would then run down through one of the runways to its nest chamber, dragging the recorder and the metal wire after it. Sometimes the animal would drag 3 to 4 meters of the cord into the burrow and sometimes only 1 meter, depending on whether it took a long or short runway to the nest chamber.

The recorders were taken out after 12 hours. In some cases the animal had freed itself from the recorder by biting the string tied around the tail, in other cases it stayed with the recorder. If the animal was loose, it was often possible to pull the recorder right out of the den. If not, we excavated the den, following the attached wire. The recorder was usually found together with the animal in the middle of the den in the nest chamber.

In order to record the microclimate inside the burrows during the night, the instrument was tied to the end of a stiff wire and pushed down through one of the runways as far as it would go. It was not possible to get the recorder much farther than 1 meter from the opening, and we never reached the nest chamber in this way.

Outside the dens, on the ground, the microclimate recorders could be used only in the night. The relative humidity was usually above 20% during the night. In the daytime, however, the relative humidity was often below 5%, and hair hygrometers could not be used. When measuring the microclimate during the night, the recorder was placed on an open wire mesh one inch above the soil surface.

Humidity and Temperature in the Ground

A very important factor for the humidity of the burrows is the water content of the soil, and the quantity of this water available to increase the humidity inside the burrows.

The question of the humidity of soil and the availability of the water is very complicated. What we actually needed was information on the humidity of the atmosphere in contact with the soil, because this factor and not the actual water content of the soil is the determining factor in our ecological problems. Consequently, we were able to avoid all questions of soil humidity if we restricted our investigations to *the humidity of a limited air space in equilibrium with the surrounding soil.*

Technically, we were able to record the air humidity in the soil by means of plac-

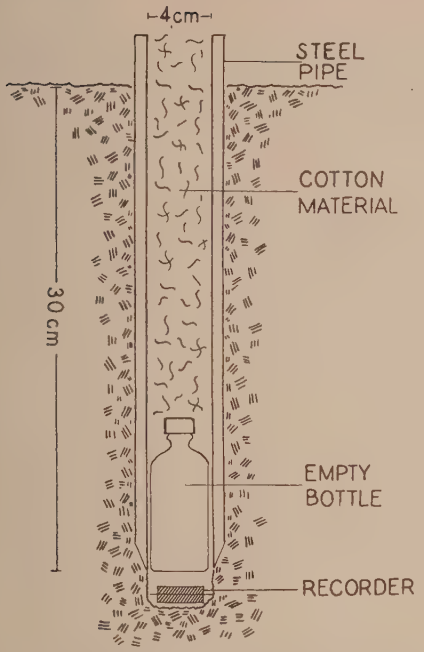

FIG. 1. Position of recorder for measurement of humidity and temperature in a closed air space in the ground.

ing microclimate recorders at different depths in the soil and record temperature and humidity continuously. We made recordings at a number of places in an area densely inhabited by kangaroo rats. The deepest holes were made by forcing a steel pipe down to the proper depth (30 cm) and removing the soil from inside the pipe by means of a fitting soil auger. The soil was removed to a little below the lower rim of the pipe, so that a small chamber was formed to accommodate the recorder (fig. 1). The pipe was plugged by a snugly fitting glass bottle, placed on top of the recorder, and ventilation of the rest of the pipe was prevented by cotton material loosely packed into it.

The shallow holes were not reinforced by steel pipe. The recorders were placed in the bottom of the hole, and the soil removed from the same level was placed around and on top of the recorder to imitate natural conditions as far as possible. The results of one typical series of measurements are given in figure 2.

The humidity increases rapidly from the surface down. There are some variations from one location to another, and on different days, especially near the surface. The variations, both in humidity and temperature, are larger near the surface than deeper down. On the whole, the variations are inconsiderable, and at 30 cm depth the air space is always 100% saturated with moisture. The temperature at this depth showed small diurnal variations around 30° C.

Considering the high soil temperature and the low humidity in the air above the ground that prevails for months, we find that the high humidity, even at a moderate depth, is surprising. The burrows often go down to a depth of roughly 1 meter, and the considerable moisture in the soil certainly must be of great influence on the burrow humidity.

HUMIDITY AND TEMPERATURE OUTSIDE THE BURROWS

The heteromyids are nocturnal in their habits. They stay in their burrows during the daytime. In the night they come out to feed and collect food which they carry to their dens. How many hours an individual stays outside its burrow is not known, but several hours of the night may be spent in the burrow. It is, therefore, of importance to measure the microclimate in the burrows during the day and night, and on the ground outside the burrows during the night.

The microclimate was recorded one inch above ground during the night over a period from the middle of May until the end of June, 1948. The results in figure 3 are given in terms of absolute humidity. The minimum and maximum in absolute humidity are given for each night for which it was recorded.

The absolute humidity in the dry nights is approximately 3 mg H_2O per liter air as calculated from relative humidity and temperature measurements. The rela-

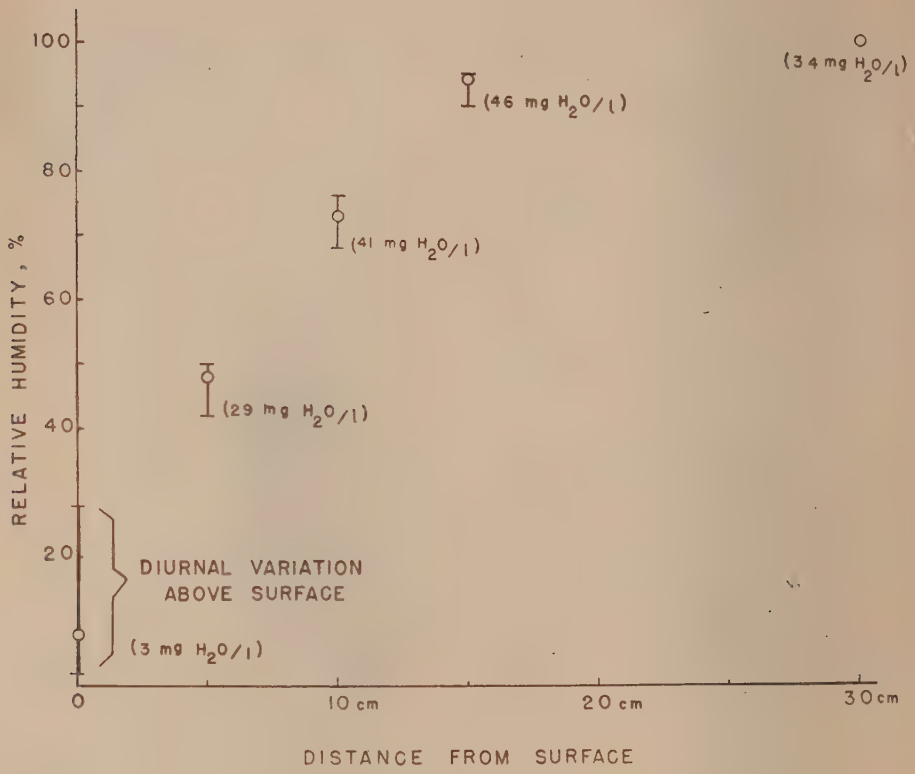

FIG. 2. The increase in relative humidity of the air with increasing depth in the ground down to 30 cm where the air is saturated with water vapor. It will be noticed that there is a higher absolute humidity closer to the surface, even though the relative humidity is lower.

tive humidity was usually between 20% and 30%. After a rainy day (6 June) the humidity was higher for several days. One day after the rain, the relative humidity in the night (7–8 June) still was 59%, but in two more days it was down to the normal very low values. There also seemed to be a higher humidity just preceding rain.

In figure 4 the variations in temperature and relative humidity are given for one night (13–14 June). It is shown as an example of the normal changes in temperature and humidity during a night in the desert at that time of the year.

The relative humidity is considerably lower during the day than during the night in the desert. The very low relative humidities during the day could not be recorded with the hair hygrometer. The determinations were made with a sling psychrometer. The results are listed in table I. Relative humidities as low as 2%, or lower, were measured. "Absolute humidities as low as less than 1 mg H_2O per liter air were found. (Low psychrometer readings are relatively very inaccurate, and the reader should be cautioned against accepting our figures as accurate determinations of absolute humidity.)

MICROCLIMATE IN THE BURROWS

The burrow of *Dipodomys spectabilis* is described by Vorhies and Taylor ('22) as "a labyrinthine underground den in which the nest is usually at the end of a blind tunnel at an average depth of nearly

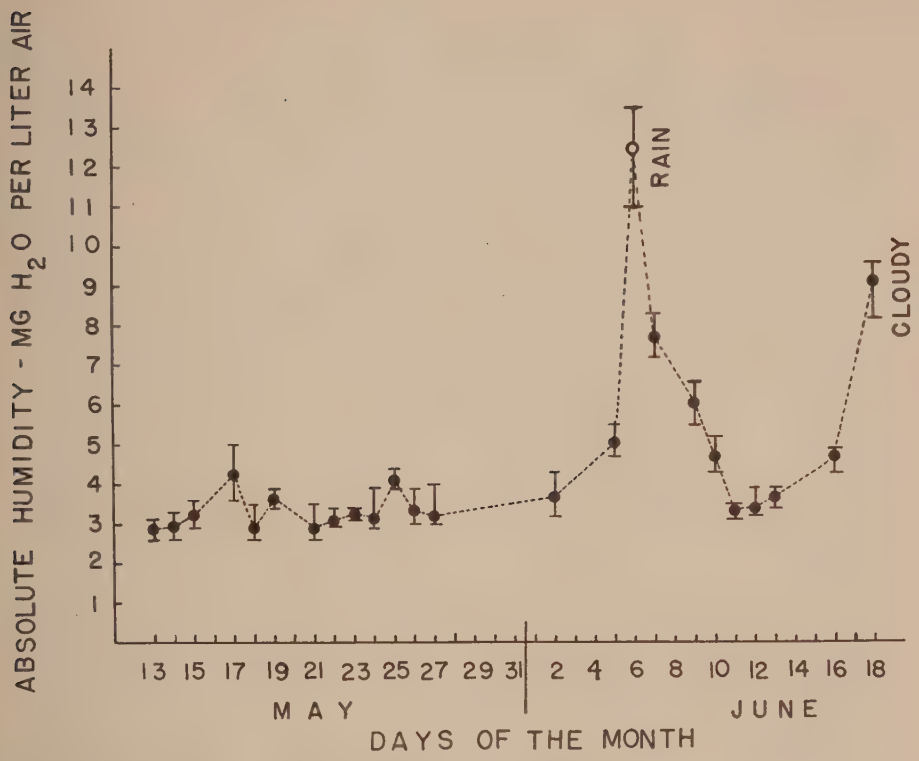

FIG. 3. The absolute humidity at the surface of the ground during the night in May and June 1948.

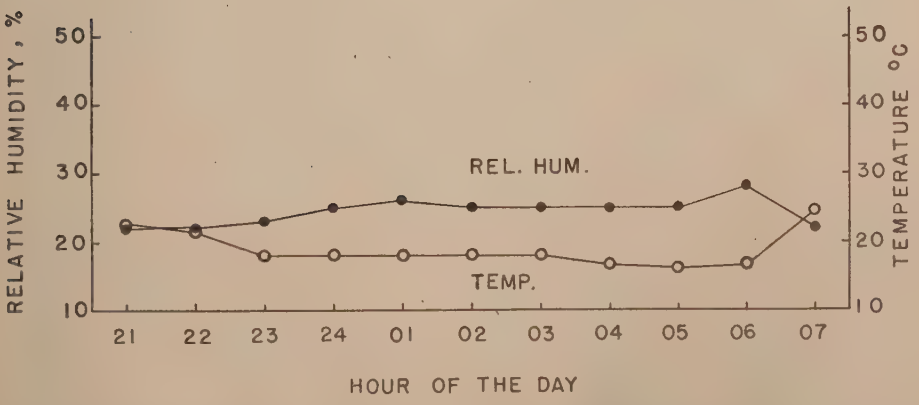

FIG. 4. Variations in the microclimate at the surface of the ground during one night. The highest relative humidity was recorded just before sunrise (28% rel. hum., 16.5° C). The dew-point may be calculated to be − 3° C, which shows that the chance for formation of dew is negligible.

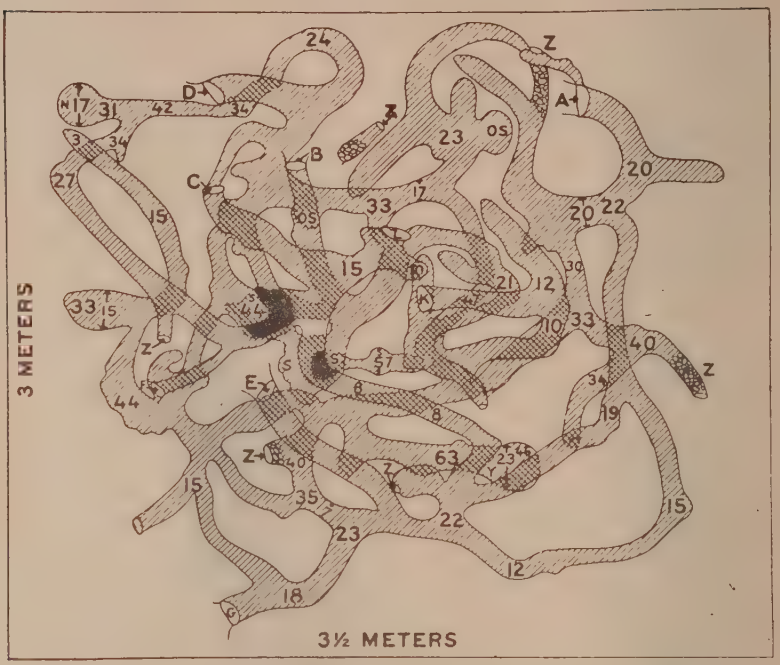

FIG. 5. Diagram of a typical den of *Dipodomys spectabilis spectabilis* (from Vorhies and Taylor). Double shading indicates where one portion of tunnel lies above another and solid black a three-story arrangement; A, B, C, etc., active openings to the surface; figures without arrows, depths in centimeters to tunnel roofs; figures with arrows, tunnel width in centimeters; N, nest chamber (from Vorhies and Taylor, '22).

2 feet." About the circulation of air through the den, Vorhies and Taylor say: "Although most of the several entrances remain open by day, it is unlikely that there is much circulation of air through such a maze of passage" (fig. 5).

The microclimate was recorded in the burrows of kangaroo rats as described above. The results are summarized in table II.

The figures show that there actually is so much ventilation that there is a drying out of the den. The average relative humidity in the nest chambers is about 30%, while the relative humidity of the air space between the soil particles at the same depth, but in closed holes, is 100%. But even though there is some drying out of the nest, the amount of water vapor in the burrows is from 2 to 5 times as great as in the outside air.

TABLE I. *Temperature and humidity in the outside air during daytime*

Date 1948 June	Time	Temperature °C	Relative humidity %	Absolute humidity mg H_2O per liter air
11	0850	29.0	10.0	2.8
	1850	33.3	5.0	1.8
12	0800	22.3	8.5	2.3
	0830	30.6	8.0	2.5
	1405	34.5	8.0	3.0
	1810	34.1	2.0	0.7
	1925	30.6	1.0	0.4
13	0850	30.5	5.0	1,5
	2025	28.5	8.0	2.2
14	0800	29.8	12.0	3.4
	1730	34.4	5.0	1.9
16	1000	31.7	8.0	2.6
17	1820	34.4	5.0	1.9
18	1835	30.8	16.0	5.1
19	1155	33.3	9.0	3.2
	1330	33.9	13.0	4.7
	2240	22.8	10.0	2.0
22	1055	29.4	32.0	9.4
	1950	26.7	38.0	9.7
23	0830	25.5	44.0	10.3

TABLE II. *Microclimate in burrows of* Dipodomys spectabilis *recorded during daytime*

Date 1948 June	Hour of day	Readings in burrows of *Dipodomys spectabilis*					Simultaneous outside readings
		Temperature maximum °C	Temperature minimum °C	Relative humidity maximum %	Relative humidity minimum %	Absolute humidity mg H_2O per liter air, average	Absolute humidity mg H_2O per liter air, average
3	1000–2000	31.0	26.0	31	22	7.3	
6	1200–1800	30.5	23.5	57	45	11.3	12.7
							Rain
6	1200–1800	27.0	23.5	62	46	13.1	12.7
8	1000–2000	27.5	25.5	42	45	11.1	—
12	1000–1900	35.0	28.5	26	18	7.4	2.0
12	1000–1800	32.0	26.5	28	22	7.3	2.0
12	1000–1800	33.5	28.5	24	18	6.7	2.0
13	0900–1900	34.0	26.5	27	21	7.1	1.7
13	0900–1900	28.5	27.5	37	33	9.9	1.7
17	1200–1700	29.5	26.5	57	45	13.5	1.9
18	1100–1900	32.0	29.5	53	39	13.6	5.1
18	1100–1900	29.0	28.0	28	28	7.8	5.1
19	1230–2230	30.5	29.0	37	37	11.0	3.3
22	0900–2000	31.0	29.5	37	33	11.3	9.6

The microclimate was also recorded in the burrows during the night. This was done by pushing the recorder into the burrow by means of a stiff wire. In most cases, it was only possible to push it less than one meter into the runway. Table III gives the results. The humidity in the runways is considerably higher than outside on the ground. Figure 6 illustrates the variations in absolute humidity during one night inside and outside the burrow of a *Dipodomys spectabilis*.

A few records were made in the burrows of *Dipodomys merriami*. The dens in which *D. merriami* live are shallower, much less complicated than the dens of *D. spectabilis*. They have only a few entrances and the runways are narrower than in the *D. spectabilis* dens (fig. 7). Besides a main burrow, the *D. merriami* has several escape holes. Without excavation, it is often very hard to tell from outside whether a hole is an escape hole or the main burrow. It is therefore possible that some of the records (see table IV) were made in escape holes. In all the cases the animal had chewed itself loose from the instrument.

Some of the burrow temperatures found are obviously too high to be tolerated by the animals. Laboratory tests for the tolerance of *Dipodomys* to high

TABLE III. *Microclimate in burrows of* Dipodomys spectabilis *during night. Measured about 1 meter from external opening*

Date 1948 June	Hour of day	Readings in burrows of *Dipodomys spectabilis*					Simultaneous outside readings
		Temperature maximum °C	Temperature minimum °C	Relative humidity maximum %	Relative humidity minimum %	Absolute humidity mg H_2O per liter air, average	Absolute humidity mg H_2O per liter air, average
9	2100–0700	29.0	22.5	40	31	8.4	6.1
10	1900–0600	34.5	29.5	45	28	12.5	5.3
11	2000–0700	30.0	27.5	54	35	11.4	3.7
13	1900–0700	33.5	29.0	19	17	5.7	3.9
18	2000–0700	31.5	27.0	33	23	8.0	8.8

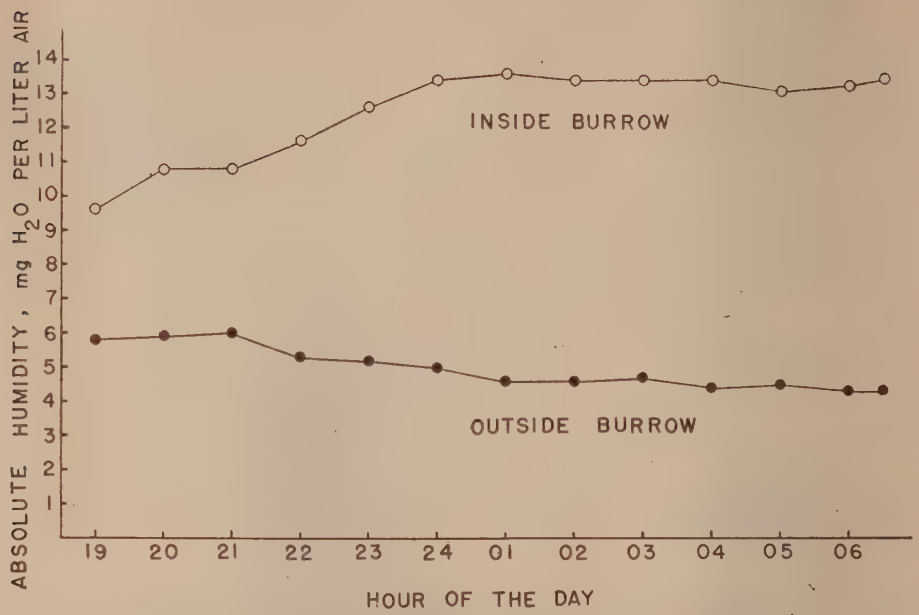

FIG. 6. Absolute humidity inside and outside a burrow of *Dipodomys spectabilis*. The absolute humidity is considerably higher inside the burrow than outside.

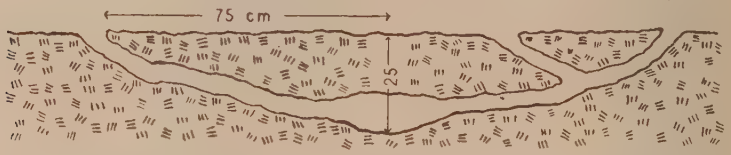

FIG. 7. Diagram of a burrow of *Dipodomys merriami*. These burrows are simple as compared with the elaborate dens of *D. spectabilis*.

temperatures showed that they cannot survive temperatures much above 38° C for any long periods. It is therefore unlikely that the holes where temperatures higher than 38° C have been recorded were the main burrows.

The variations in temperature are larger in the shallow *D. merriami* dens than in the deeper *D. spectabilis* dens, as seen from the greater range of the figures in these observations, but the moisture is about the same as in the *D. spectabilis* dens. In a single den, a very high relative humidity was found (average 84%, range 62% to 91%). The ventilation in that particular den may have been very small or the hole may have been new, and it is probable that the burrow had only one entrance.

DISCUSSION

The microclimatic investigation shows that even during the driest season of the year the soil in the Arizona desert contains enough water to keep a closed air space in the ground at a depth of 30 cm saturated with water vapor. The air space in the burrows is not saturated with water vapor, but its moisture content is 2 to 5 times as high as the atmosphere outside the burrows.

The moisture content of the air in the burrows is an important factor in the water economy of the desert rats. We

TABLE IV. *Microclimate in burrows of* Dipodomys merriami

Date 1948 June	Hour of day	Readings in burrows of *Dipodomys merriami*					Simultaneous outside readings
		Temperature maximum °C	Temperature minimum °C	Relative humidity maximum %	Relative humidity minimum %	Absolute humidity mg H_2O per liter air, average	Absolute humidity mg H_2O per liter air, average
3	1000–1700	35.5	29.0	25	20	7.7	
8	1000–1900	31.5	25.5	62	44	15.0	—
11	0900–1800	35.5	28.0	50	23	12.5	2.3
14	0900–1800	39.0	28.0	27	13	6.7	2.6
17	1200–1800	39.0	32.0	48	31	14.9	1.9
17	1900–0700	43.5	33.0	91	62	36.8	4.7

can assume that the *Dipodomys,* like other mammals, expire air that is saturated with moisture at a temperature slightly below that of the body. Dill ('38, p. 26) says that the expired air is saturated with water vapor at about 33° C. Normal body temperature in *Dipodomys merriami* is 36–37° C, and we will base our calculations on Dill's figure for temperature of expired air. Air saturated with water vapor at 33° C contains 35.3 mg of water per liter air. A *Dipodomys* which is breathing completely dry air will therefore lose about 35 mg of water per liter air expired. If the animal breathes desert air with a moisture content, as we have measured it during the daytime, of about 2 mg water per liter air, it will lose approximately 33 mg of water per liter air expired. If, however, the animal stays in the burrow, the air it inspires will contain roughly 10 mg of water per liter, and the animal will lose only about 25 mg of water per liter expired air, or 24% less than in the first case.

In the water economy of the animals, this saving is very important because it determines whether the production of metabolic water will lead to an ultimate loss or gain. A common view is that metabolic water is of course useful but not a very decisive factor, since the metabolism, in addition to formation of water, involves respiration, i.e., evaporation from the lungs. The value of metabolic water is discussed, e.g., by Howell and Gersh ('35), who say: "Factors intimately connected with the rate of metabolism include rate of respiration, body temperature and activity. It is obvious that the increase of any one of these to secure more metabolic water will also increase the rate of water loss from the body, and a sort of vicious circle would then ensue. On the whole, it would seem that an animal on a dry diet gets along better with a slow rate of living, and hence lower metabolism, than one that has to sacrifice much water by loss from the body concomitant to high metabolism. Hence metabolic water is a critical factor to be accepted thankfully, like free water in the food, but its increase proves too expensive an undertaking to be practicable."

We cannot quite agree in this viewpoint. The evaporation from the lungs is influenced by the humidity of the inspired air and the ventilation of the lungs, and whether or not the formation of metabolic water will lead to an ultimate loss or gain can easily be calculated. The

TABLE V. *Amounts of water formed and oxygen used when pure foodstuffs are metabolized*

	Carbohydrate	Fat	Protein
Gram of water formed per gram foodstuff metabolized	0.556	1.071	0.396
Liter oxygen used per gram foodstuff metabolized	0.800	2.01	0.95
Mg water formed per ml oxygen used	0.69	0.53	0.42

amount of water formed per gram of foodstuff metabolized is shown in table V. In the same table is shown, also, the amount of oxygen used per gram foodstuff combusted; and finally the amount of water formed per ml of oxygen used.

Using the figures for the composition of grain from a nutritional chart (Heinz, '46), we can calculate the amount of water formed per ml oxygen used when grain is metabolized. Table VI shows the figures.

TABLE VI. *Composition of the common grains and the amount of water formed by their metabolism. Calculated in relation to the amount of oxygen required for the combustion in the body*

	Composition of grains			mg water formed per ml oxygen used
	Carbohydrate	Fat	Protein	
Barley	78.3	1.0	8.2	0.66
Oats	67.0	7.4	14.2	0.63
Wheat	50.2	5.2	16.0	0.62

We will now compare the figures for the amount of water formed by the metabolism with the figures for the amount of water lost by evaporation from the lungs. With 16% oxygen in the expired air (normal value for man and many other mammals) 50 ml oxygen is taken up per liter air expired. When corrected for temperature, vapor pressure and barometric pressure this gives 42.4 ml O_2. If the animal breathes completely dry air, it will lose 35.3 mg of water per 42.4 ml oxygen taken up, or 0.83 mg of water per ml oxygen. This figure is larger than the figures shown in table V for the amount of water formed per ml oxygen used when grain is metabolized. This means that an animal breathing dry air will lose more water by evaporation from its lungs than is formed by its metabolism.* In other words, in that particular case, the formation of metabolic water will lead to an ultimate loss of water.

If the animal breathes air containing 10 mg of water per liter (as is found in the burrows), the loss of water from the lungs will be 0.61 mg per ml oxygen taken up. In this case, water is gained by metabolism and an increase in the metabolism will lead to an increase in the water gained.

The moisture content in the atmosphere outside the burrows during the night was, in the dry season, about 4 to 5 mg of water per liter air. Under these conditions the water loss from the lungs will be about 0.72 mg per ml oxygen. The amount of water lost slightly exceeds the amount of water gained. As the animal spends less time outside the burrow than inside, the overall picture will show a gain in water by metabolism.

However, this whole discussion was built upon the validity of certain assumptions. In order to reach exact conclusions, these assumptions will have to be proved. Certain factors may differ in a direction more to the advantage of the animal. In fact, we have experimental results indicating a higher degree of utilization of the alveolar oxygen. Later publications will deal with these matters.

SUMMARY

The humidity and temperature have been recorded in the burrows of the desert rodents *Dipodomys spectabilis* and *Dipodomys merriami*. The observations were made in Southern Arizona during the driest time of year.

It was found that the humidity inside the burrows always is considerably higher than outside. If the animals were breathing the air outside the burrows with its very low moisture content, the rate of evaporation from the lungs would exceed the rate of formation of metabolic water, with the result that the animals would lose water by their metabolism.

By calculations, it is shown that the higher humidity in the burrows is very

* This statement is only valid if the assumptions made are valid, namely, that water content of the expired air corresponds to saturation at 33° C and that the animal does not utilize the alveolar oxygen to a greater degree than other mammals. Laboratory experiments showed that heteromyids actually lose less water from the lungs than assumed here.

significant for the water balance of the animals. The formation of metabolic water will, when the animals breathe the fairly moist air in the burrows, lead to an ultimate gain in water.

Acknowledgments

This work was supported by the Office of Naval Research as part of projects for physiological field research initiated by Dr. L. Irving. We gratefully acknowledge valuable advice and suggestions from Dr. August Krogh, who visited the U. S. A. in early summer 1948 and took part in some of our field work. Dr. Horace Haskell, University of Arizona, helped us excavating rodent burrows. Mr. R. Price, Director, Southwestern Forest and Range Experiment Station of the U. S. Department of Agriculture, Tucson, Arizona, kindly provided working space at the Santa Rita Experimental Range, Arizona.

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LIMNOLOGICAL STUDIES OF LOUISIANA LAKES
1. LAKE PROVIDENCE[1]

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NATURE OF THE INVESTIGATION

The primary purpose of the lake studies described here was the investigation of the possible causes of the late-summer fish mortality which had occurred repeatedly at Lake Providence previous to 1945. A considerable amount of time during 1945–46 was devoted to studying the "normal" limnological characteristics of the lake. A resume of these general features is here presented as a contribution to limnological knowledge of a region which has received but scant attention in the past.

Since the basin was unmapped, systematic soundings were made for the purpose of developing a rough contour map of the basin. Stations were then established at representative spots at which regular determinations of water temperature, dissolved oxygen, carbon dioxide, pH and alkalinity were made. Plankton collections were also made regularly at these stations, including surface net and nannoplankton collections, and tows from various depths. Dredge samples were taken at stations representative of the various depths and bottom types. The field methods employed, the chemical tests, and the laboratory processing methods were all standard procedures as described in Welch ('48). Results of these studies are presented in appropriate sections of this report.

DESCRIPTION OF THE LAKE AND DRAINAGE BASIN

Lake Providence, in East Carroll Parish, northeast Louisiana, is an old river-lake approximately five and one-half miles in length, averaging one-third mile in width, and occupying an area of about 1,380 acres. The basin is essentially simple and regular, showing unmistakable evidence of its origin as a stream channel. The west slopes are, as a consequence of the former direction of current, the most steep. Sedimentation is most pronounced at the upper and lower ends of the basin, particularly the former. The only shoals are located in these areas and in the "Chute," a narrow, shallow arm extending northwestward from the lower part of the basin. The maximum depth of the lake is approximately forty feet; the average depth about seventeen feet.

Lake Providence is situated in the Mississippi River flood plain, the soil being typical dark silty sand and clay. The native vegetation of the area is Red Gum–Water Oak (Winters, *et al,* '38); although the principal woody species bordering the basin are old cypress, with a lesser number of sycamore and an understory of willow. The lake basin is almost entirely surrounded by wooded shores rising steeply from the water's edge. The lake floor is almost exclusively of mud; only the zone above the two meter contour is composed of fine sand or sandy mud, with occasional areas of compact clay soil. There is, of course, considerable organic detritus mixed with the bottom soil under the cypress border.

The water supply of the lake is maintained by seepage from the nearby Mississippi River; by a limited amount of slope wash; by surface run-off from the town of Lake Providence at the lake's southern end, a part of which drains into the lake; and by drainage from the area north and east of the lake by way of two inlets entering the north end of the basin.

These two inlets, Jack Falls Bayou

[1] These studies were made possible through the financial support of the Louisiana Department of Wild Life and Fisheries. The writer is especially indebted to Major James Brown, Director, and Dr. J. N. Gowanloch, Chief Biologist of the Division of Fish and Game, for the opportunity thus afforded.

and Bayou Providence, formerly drained an area of approximately 22,000 acres. With the building of a new protection levee in 1932–33, approximately half of this original drainage area was lost. At present, Jack Falls Bayou is almost completely non-functional and Bayou Providence is an intermittent stream with a significant flow only following periods of flood rain.

Lake Providence has two outlets: Baxter Bayou which runs southwestward into Bayou Macon and thence into the Tensas River; and Tensas Bayou which likewise drains into the Tensas River and thence into the Red River shortly before its junction with the Mississippi. Previous to 1923, Baxter Bayou was an inlet; in that year the channel of the stream was deepened by dredging resulting in a reversal of the direction of flow. Both of these outlets are provided with concrete concentration dams, the purpose of which is to stabilize the lake level at approximately 90 feet, Mean Gulf Level. Because of the limited area of the drainage basin and the intermittent nature of the inlets, extensive temporary variations in lake level are common. Fluctuations of as much as twelve inches have been noted within the space of forty-eight hours. Moreover, since precipitation in this area is most abundant from December through May, the lake level may be much higher in early summer than in late fall.

Aquatic Vegetation

The paucity of the aquatic flora of Lake Providence, aside from phytoplankton, was a striking feature. A "hard-water" lake of this type might be expected to support an abundant and varied plant population; the aquatic vegetation, however, proved to be scanty and restricted to a few areas. Probably this was due to the relative steepness of the border slopes of the basin which severely restricted the amount of shoal area, and to the abundant phytoplankton which not only limited light penetration but also was a considerable drain on the available supply of nutrients.

The most abundant single species, and the only submerged aquatic present, was coontail, *Ceratophyllum demersum.* In the summer of 1945 this plant was very abundant in the upper "chute" where it was associated with a sparse surface covering of duckweed, *Spirodela polyrhiza.* Masses of coontail frequently drifted into the main body of the lake but it did not appear to be established at any other point. The abundance of Ceratophyllum was noticeably less in the summer of 1946. This was perhaps due to the excessive silting which occurred in this shallow arm of the lake during the previous winter and spring as a consequence of the abnormally high precipitation of that period.

A few types of emergent aquatics were observed in occasional scattered patches. These included cat-tail (*Typha latifolia*), lizard-tail (*Saururus cernuus*), and water primrose (*Jussiaea diffusa*). The north end of the basin, particulary the intermittent inlets, Bayou Providence and Jack Falls Bayou, was extensively grown up with cut grass (*Zizaniopsis miliacea*). It appears that cut grass is invading the basin from its northern inlets.

Thermal Characteristics

The annual thermal cycle of Lake Providence differs from that of typical thermally stratified lakes of the temperate zone chiefly in the absence of a winter stagnation period. Below-freezing temperatures in this area are relatively uncommon and usually of short duration; consequently no ice cover forms over the lake.

While this means that there can be no typical winter stagnation period, it does not exclude the possibility of thermal stratification of the lake during the summer months. That such stratification occurs is demonstrated by the records of water temperatures obtained during the fifteen month period of the present inves-

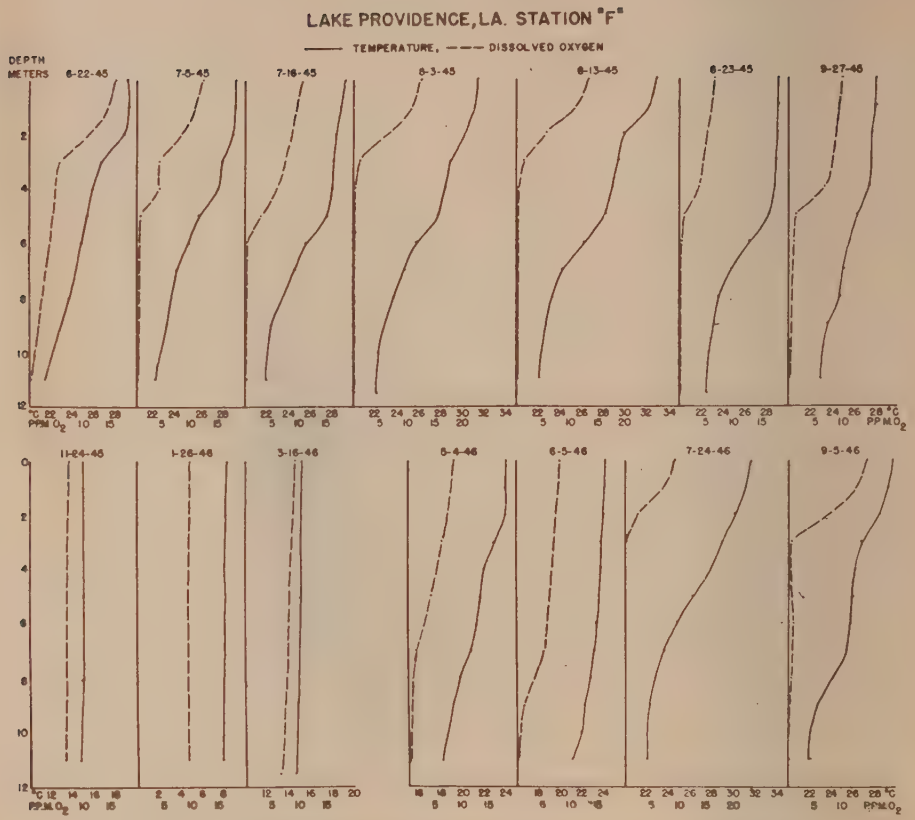

FIG. 1. Water temperature and dissolved oxygen curves, Station "F".

tigation. These data, taken at Station "F" in the deepest part of the basin, are presented in graphic form in figure 1.

It will be noted that Lake Providence displays one period of thermal stratification from May or June through September, followed by a period of continuous circulation from October through April. The thermocline, distinguishable in June, 1945 as a thin stratum with its upper limit at about two meters, subsequently became more or less stabilized between five to eight meters. Thermal stratification was abnormally delayed the following summer due to exceptionally abundant late spring precipitation, and the washing out of the Baxter Bayou dam with the consequent draining off of a considerable volume of surface water. The phenomenon of secondary thermocline formation was frequently observed in localized areas and is illustrated in figure 1 in the record for August 13, 1945.

Observations extending over a fifteen month period indicate that water temperatures do not normally fall as low as 4° C. Both surface and bottom temperatures show a wide annual range, the extremes in surface temperatures at Station "F" being 33° and 8.3° C in August and January, respectively; the bottom temperatures 23° and 8° C in September and January.

CHEMICAL CHARACTERISTICS

(1) Dissolved oxygen:

Figure 1, previously cited, shows the annual dissolved oxygen cycle in the

deepest part of the lake basin. Depletion of dissolved oxygen in the lower waters was usually complete by July, the anaerobic conditions persisting in the hypolimnion until late September. From November through March surface and bottom samples showed nearly uniform concentrations of dissolved oxygen.

Surface oxygen, on the other hand, was consistently above the saturation point during the summer months. Ordinarily, surface oxygen concentrations during the period of summer stratification ranged from 10 to 16 parts per million; one instance of 18.85 ppm. (245% saturation) was recorded. These conditions of supersaturation were associated with the heavy phytoplankton population.

Although marked differences in the oxygen content of the upper and lower levels of the thermocline stratum are to be expected, it is unusual to find such a rapid vertical decline in dissolved oxygen as is characteristic of Lake Providence during the summer months. Instances of a drop of as much as 7 ppm. per meter were not unusual, and one record of a decline from 9.8 to 0.9 ppm. within a vertical distance of one meter was noted. In many cases this rapid decline occurred above the upper limit of the primary thermocline, an indication that the epilimnetic waters of the lake did not circulate freely at all times. This condition was not unexpected in view of the long, narrow, arc-shaped lake basin; the direction of the prevailing winds in summer which blew across the short axis of the basin; and the nearly unbroken cypress border of the lake which reduced wind action by mechanical interference.

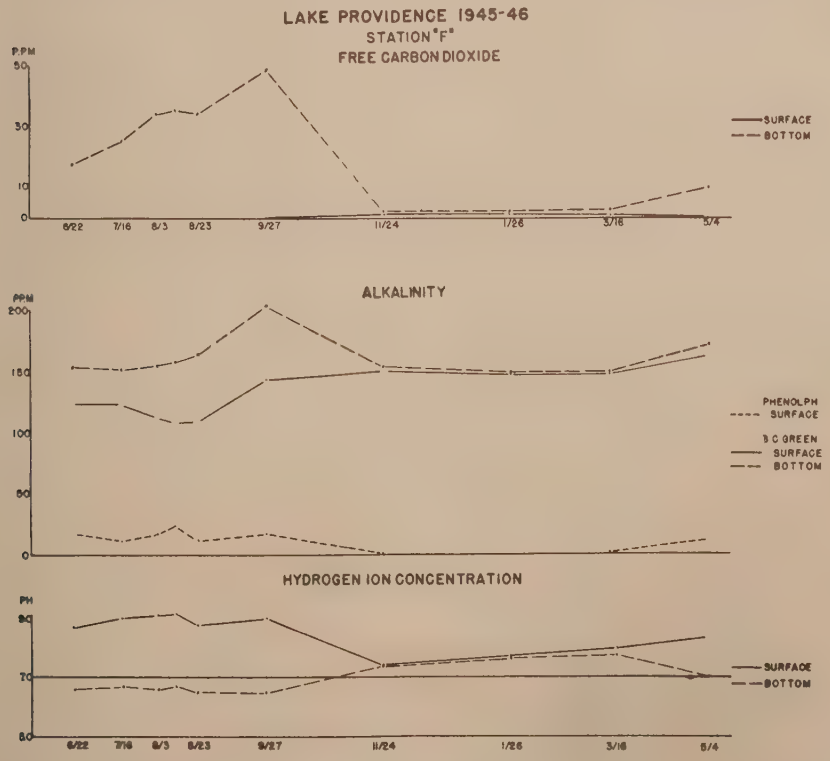

FIG. 2. Annual cycle of free carbon dioxide, alkalinity, and hydrogen ion concentration, Station "F".

(2) Free carbon dioxide:

The surface waters of Lake Providence (see fig. 2) invariably tested negatively for free carbon dioxide at all stations throughout the summer season. Water samples collected from just above the bottom, however, did contain appreciable amounts ranging from 10 to 18 ppm. in late June and increasing to as high as 48 ppm. by September. During winter and early spring carbon dioxide concentrations of 1.0 to 2.5 ppm. prevailed, with little difference between surface and bottom. There was no progressive increase in free carbon dioxide throughout the winter, due to the lack of any winter stagnation period. The typical carbon dioxide gradient associated with thermal stratification was reestablished in May, 1946. Subsequent records during the summer of 1946, although not shown on figure 2, practically duplicate the determinations made the previous summer.

(3) Alkalinity:

Alkalinity was determined as "phenolphthalein alkalinity," a measure of carbonate hardness; and "brom-cresol green alkalinity," a measure of total hardness including carbonates and bicarbonates. As illustrated graphically in figure 2 (which shows the annual cycle of alkalinity in both surface and bottom waters at a typical station), carbonates were present only in the surface waters of the lake, and only there during the summer stagnation period. After the fall overturn, phenolphthalein alkalinity of the surface waters dropped to zero and no dissolved carbonates were recorded there until the reestablishment of thermal stratification in May, 1946.

Total alkalinity was invariably greater in the lower strata during the season of thermal stratification, a consequence of the utilization of the half-bound carbonates by the phytoplankton concentrated in the upper levels. This contrast in total alkalinity between surface and bottom waters increased to a maximum in late August and September when the phytoplankton population was at its maximum. Concomitantly there was a gradual increase in total alkalinity of the bottom waters throughout the summer as a result of the death of phytoplankton and the subsequent return of the soluble carbonates and bicarbonates to the lake water.

Total alkalinity became nearly uniform, top and bottom, and was essentially constant during the period of uninterrupted water circulation of late fall, winter, and early spring. The usual gradient once more became apparent with the beginnings of thermal stratification in May, 1946; and the recorded cycle during the following summer closely paralleled that of the summer of 1945.

(4) Hydrogen ion concentration:

The hydrogen ion concentration of the surface waters of Lake Providence during the summer stratification period showed an extreme range from pH 8.1 to pH 9.1, although at any one station the range was somewhat less. Variations which did occur were small and irregular. The relative stability of the hydrogen ion concentration of the surface waters during this period was probably due to the abundance of dissolved buffer substances, particularly carbonates and bicarbonates of calcium and magnesium.

The hydrogen ion concentration of the hypolimnion during the same period showed a much smaller range, the extremes being from pH 6.8 to pH 6.5. This slightly acid reaction was due to the presence of free carbon dioxide. There was no clear indication of any tendency toward a condition of increasing acidity during the summer stagnation period.

With the upsetting of thermal stratification and initiation of the winter circulation phase, surface and bottom waters became nearly uniform in pH. This condition persisted from November, 1945 until early May, 1946. The hydrogen ion concentration of surface and bottom waters during this period ranged between

pH 7.4 and pH 7.9. In May, 1946 the usual gradient had become reestablished with the surface showing a pH of 8.3 and the bottom waters a pH of 7.0. This divergence became more pronounced as the summer progressed, paralleling the conditions of the previous summer.

(5) Total dissolved solids:

Because of technical difficulties, determinations of total dissolved solids were not begun at Lake Providence until August, 1945. From this date until September, 1946 a total of eight such determinations (see table I) were made on the surface water collected at Station "F".

TABLE I. *Total dissolved solids—surface—Lake Providence*

Date	ppm.
August 22, 1945	130
November 23, 1945	179
January 25, 1946	187
March 16, 1946	194
May 4, 1946	199
June 5, 1946	195
July 25, 1946	163
September 5, 1946	120

Throughout the period of free circulation total dissolved solids were fairly uniform in quantity. During the summer stagnation period, especially towards the end, total dissolved solids in the surface waters were much less, understandably so since carbonates and bicarbonates constitute a large proportion of such materials and these were markedly reduced during this period through the activity of the plankton algae.

(6) Bottom deposits:

A rough determination of the organic material present in the bottom deposits of Lake Providence was attempted by drying samples of the mud (at 103° C), igniting the sample in an electric muffle for one hour at 600° C, and recording the percentage of organic matter as the loss of weight on ignition. Nine such samples from the deepest part of the lake (12 meters), collected at intervals during the period June, 1945 through September, 1946, were remarkably uniform in their content of volatile material, the loss of weight on ignition varying from 11.64% to 13.68% of the dry weight of the sample.

PLANKTON [2]

(1) Myxophyceae: In numerical preponderance the blue-green algae exceeded all other forms, whether considered individually or collectively. Of particular abundance was the genus Chroococcus, the species *C. minutus* (Kutzing) Nagelli, *C. dispersus* (v. Keissler) Lemmermann, and *C. dispersus minor* Smith being identified. Occasional individuals of *C. giganteus* W. West were also observed. This genus, present throughout the entire year, attained its maximum population in September, 1945. Of probably greater importance from the point of view of total volume was the genus Anabaena, particularly *A. spiroides* Klebahn. The spiral filaments of this form were usually present in abundance except during the winter months, and the species reached a maximum population of over 4 million filaments per liter in July, 1946. Frequently during the summer of 1945, windrows of blue-green algae were observed in localized areas; at times it formed a heavy green scum on the surface of the water. Microscopic examination of this scum showed it to be composed principally of Anabaena. The third blue-green of particular abundance was *Lyngbya limnetica* Lemmermann. This species "bloomed" in July, 1946. Occurring simultaneously as it did with an Anabaena population maximum, the high turbidity produced was reflected by a Secci disc reading of only 50 centimeters, although it had been 120 centimeters during the previous month.

(2) Chlorophyceae: The green algae, while less abundant than the blue-green, included at least nine genera. Only one

[2] In the following brief discussion of the more common surface net and nannoplankton organisms, the nomenclature is that of Smith (1920, 1933) for the algae, and of Harring (1913) for the rotifers.

was present throughout the entire year; this was the genus Scenedesmus, especially *S. quadricauda* (Turpin) de Brebisson. In common with most of the other green algae, Scenedesmus showed a relatively greater abundance during the winter months.

(3) Bacillareae: The frequently encountered observation that diatoms dominate the winter plankton was not borne out in the present instance. Diatoms were found to be of relatively little importance, both numerically and in total number of species, at all seasons in Lake Providence. Moreover, the winter collections showed few or no diatoms present. Synedra was the only genus of diatoms ever present in any considerable numbers.

(4) Mastigophora: The flagellate protozoa were represented throughout the entire year, although in numerically small quantities, by both Dinoflagellates (Peridinium and Ceratium), and by Phacus and other euglenoid flagellates.

(5) Sarcodina: The amoeboid protozoa were very sparsely represented; during the winter months they were entirely absent. The principal type was the shelled form, Difflugia.

(6) Rotifera: Rotifers were important in that they represented the predominant zooplankton type. Considered as a group, the rotifers did not exhibit the tremendous population fluctuations shown by some of the phytoplankters. There was one rotifer maximum in mid-July, 1945 and a somewhat lesser one in March, 1946. When the counts of individual species are considered, however, it is interesting to note that one rotifer may dominate at a given time, and be but sparsely represented at other seasons. The most important (numerically) of the rotifers incuded *Polyarthra trigla* Ehr.; *Trichocerca longiseta* (Schrank); Brachionus, especially *B. angularis* Gosse; and Snychaeta. Polyarthra were few in number, although almost continuously represented, from June, 1945 until June, 1946 when the species reached a population of 241 per liter. Trichocerca showed population maxima in late June and early July, 1945 with a second lesser maximum in September of the same year. It was absent, or very nearly so, during all the winter months. Brachionus was the single most abundant genus, with a count of 715 per liter on July 16, 1945; the genus was fairly well represented in all the other collections except those made during the winter. Synchaeta furnished an interesting contrast in that it was absent or rare during the warmer seasons, but attained a maximum population of 260 per liter in November, 1945.

(7) Crustacea: An unexpected finding was the nearly complete absence of Cladocera at all seasons of the year. Plankton crustacea were represented entirely by copepods (*Cyclops* sp. and *Diaptomus* sp.) and their larvae. Naupleus and metanaupleus larvae occurred in small numbers in all surface net plankton collections; they were relatively more abundant during the period of warmer water temperatures. Adult copepods were always very few in number in the surface plankton and were found there only during winter and early spring before thermal stratification had become established.

Bottom Fauna

Nature of the bottom deposits:

The approximate total areas of lake bottom falling within each depth zone (2 meter contour interval) were determined by the use of a planimeter on a large scale map of the lake basin. These areas are listed in table II.

Table II. *Areas of depth-zones, Lake Providence*

Depth-zone (*meters*)	Acres	Square meters	% of total area
0–2	231.1	935,238.6	17
2–4	259.3	1,049,361.2	19
4–6	232.2	939,690.2	17
6–8	211.8	857,133.4	15
8–10	204.2	826,377.0	15
10–12 plus	241.9	978,945.1	17
Total	1,380.5	5,586,745.5	100

The character of the bottom deposits was strikingly uniform over the entire basin. Below four meters, practically the only type of bottom encountered was mud; above four meters there was a gradually increasing amount of fine sand mixed with the mud; and above the two meter contour, a fine sand bottom predominated. Local areas of compact clay bottom were occasionally encountered down to depths of four meters, but these areas were of such limited extent that they did not materially alter the average character of the bottom type of a given depth zone. Organic detritus was a common constituent of the bottom deposits in water of a depth of four meters or less. The source of this detritus was evidently the trees which bordered the basin; little, if any, was derived from rooted aquatic vegetation since the latter was extremely scanty in amount and very sparsely distributed.

Characteristics of the summer bottom fauna:

It is common practice to recognize three major life-zones on the lake floor of thermally stratified lakes: the littoral, sublittoral, and profundal. As generally employed the littoral zone refers to the lake bottom between the water's edge and the lakeward limit of rooted aquatic vegetation; it usually corresponds to the region of the epilimnion. The profundal zone extends from the greatest depths up the slope to a level corresponding to the upper limit of the hypolimnion. The sublittoral zone is a poorly defined region lying between these two and, in general, in contact with the thermocline.

With reference to the qualitative distribution of benthic organisms in these three zones, it is obvious that the diversified physical and chemical conditions characteristic of the littoral zone should result in a qualitatively diversified littoral fauna. Numerous studies on American lakes have demonstrated that this is indeed the case (cf. Muttkowski, '18; and Baker, '18); the zone of greatest diversity of species generally occurs in the region of 0.5 to 3.0 meters. In Lake Providence by far the greatest number of types were found above the four meter contour, the approximate lower limit of the littoral zone. Such insect forms as Trichoptera larvae and Ephemerida larvae were, in fact, confined to this region. Others, including chironomids, ceratopogonids, and Chaoborus, were well represented here. Mollusca were common and, with one exception, were confined to the littoral zone. Annelids, both Oligochaeta and Hirudinea, were also numerous though by no means confined to this area. Amphipods (Hyalella) and coelenterates (Hydra) were but sparsely represented and were restricted to the littoral zone.

With increasing depth beyond the littoral zone the number of benthic species usually diminishes, often rapidly. Within the sublittoral zone of Lake Providence practically all the types mentioned above dropped out, except for chironomids, Chaoborus, and oligochaete worms. The profundal bottom fauna, found below the eight meter contour, was made up entirely of these three groups plus one collection each of snails and leeches.

A graphic representation of the depth-distribution throughout the summer months of the three groups of organisms almost invariably present at all depths is shown in figure 3.

For Chaoborus, the average maximum population density throughout the summer months was found on mud bottom at five to seven meters depth. At seven meters the population dropped off, to rise to a lesser peak in the deepest profundal areas.

The aquatic earthworms (Oligochaeta) showed two zones of high population density during the summer months, at one meter and seven meters respectively. Dredge samples from the profundal zone consistently ran relatively low in numbers of oligochaete worms. That the paucity of Oligochaeta in the profundal zone of Lake Providence may be related to summer oxygen depletion in this zone is sug-

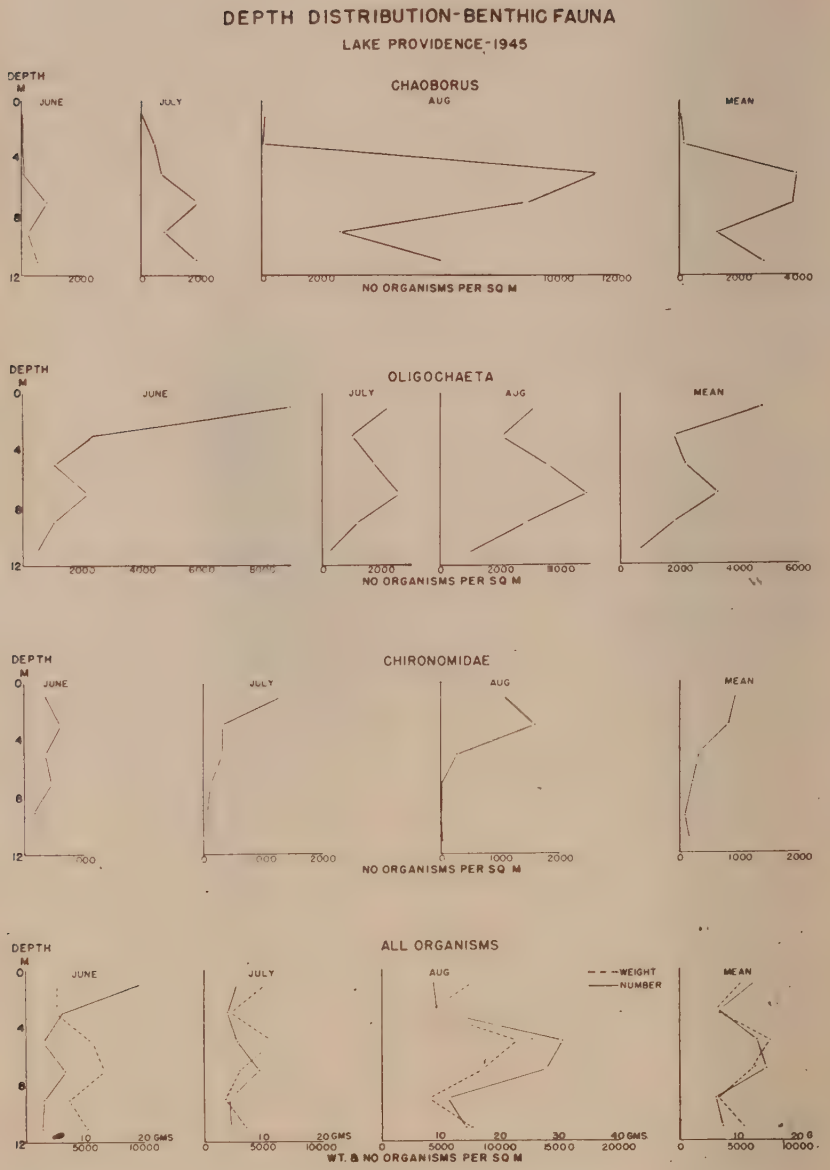

FIG. 3. Depth-distribution of benthic fauna; summer, 1945.

gested by the fact that at the end of September, 1945 (with the fall overturn in progress) the population there rose to over 6,000 individuals per square meter and remained at a very high level until March of the following year. No specific determinations of Oligochaeta were made, although Tubificidae were particularly numerous and Lumbriculidae common.

During the early part of the summer, chironomids were more or less uniformly distributed from the upper littoral to the

TABLE III. *Benthic productivity, Lake Providence* (Expressed as kilograms drained wet weight)

Depth zone	June	July	August	Mean
0–2 m	5,143.8	9,820.0	14,309.2	9,726.5
2–4 m	5,666.6	4,617.2	8,290.0	6,191.2
4–6 m	10,618.5	11,088.3	21,424.9	14,377.3
6–8 m	11,657.0	5,228.5	14,657.0	10,542.7
8–10 m	6,197.8	3,140.2	6,611.0	5,288.8
10–12 m	10,278.9	6,852.6	14,780.0	10,670.5
Total	49,562.6	40,746.8	80,072.1	56,797.0
Productivity:	35.9 kg/acre 79.0 lb/acre	29.5 kg/acre 65.1 lb/acre	58.0 kg/acre 127.6 lb/acre	41.1 kg/acre 90.4 lb/acre

deepest profundal areas. As oxygen exhaustion in the profundal zone became more complete, the chironomid population of this zone dropped until by August they were nearly absent from both the profundal and lower sublittoral zones. At this time a rather abundant population of these forms was to be found in the littoral areas. Several types of Chironomidae were collected but the only species identified was *Chironomus plumosus* which comprised practically the entire chironomid population of the profundal and lower sublittoral zones.

A rather widely accepted concept with application to thermally stratified lakes is that of the "concentration zone." First described by Eggleton ('31) for certain Michigan lakes, it has been reported for thermally stratified lakes in a variety of localities and may be of very general occurrence (Welch, '35, p. 300; Eggleton, '34, '39). This concentration zone typically shifts up and down the slope of the lake floor with the change of seasons. It occurs in the profundal zone in early spring, moves to the upper profundal and the sublittoral in summer, and returns to the profundal zone during the autumnal overturn.

Reference to the population curves for the total number of organisms collected during the summer months of 1945 (fig. 3) reveals a zone of maximum total population at a depth of six to eight meters (lower sublittoral) during June [3] and July; this zone rose to include the four to six meter depth zone (also sublittoral) in August. It may be concluded that the concentration zone is, in general, well illustrated in the summer distribution of benthic organisms in Lake Providence.

Using the depth-zone areas as given in table II and the drained wet-weight determination of the benthic fauna, the benthic productivity of each of the depth-zones, in terms of total weight of organisms present, was calculated. Table III gives these productivity determinations for each of the three summer months, as well as the mean productivity during the entire period. As might be expected, the sublittoral zone consistently showed the greatest "standing crop" of benthos in terms of weight as well as numbers; but it is interesting to note that while the greatest average number of organisms occurred in the 6–8 meter zone, the greatest average weight of organisms was found in the 4–6 meter zone. Expressed in terms of drained wet-weight of organisms per unit area, the mean benthic productivity of Lake Providence at all depths was approximately 41.1 kilograms per acre, or 90.4 pounds per acre.

Annual cycle of the profundal bottom fauna:

Only at Station "F" were dredge samples collected regularly during the entire

[3] There was also a very large June population of very small Oligochaeta at the shallowest stations. Note the apparent discrepancy between the curves for weight and number of organisms.

annual cycle. Typically, the profundal benthic population consists of large numbers of individuals of a very few species. That this situation was characteristic of Lake Providence was evidenced by the fact that substantially the entire annual population of benthic organisms at this station was limited to three types: the aquatic larvae of two Dipterous insects (Chironomidae and Chaoborus), and aquatic earthworms (Oligochaeta). These types varied greatly in number of individuals present and in the proportion they constituted of the total population at any given time; but none of them (except Chironomidae in late September, 1945) were completely absent from the collections at any season of the year.

In addition to this qualitatively stable population of organisms, two other types were represented: one a leech and the other a fingernail clam. Each was collected on only one occasion in the entire series; and neither can, on the basis of these data, be considered an important part of the benthic population at Station "F".

A graphic representation of the constitution of the profundal bottom fauna of Lake Providence throughout the year is given in figure 4. Reference to these population curves reveals, in general, a rather scanty summer population which increased rapidly to a maximum in late fall or early winter. This winter population maximum was maintained until early

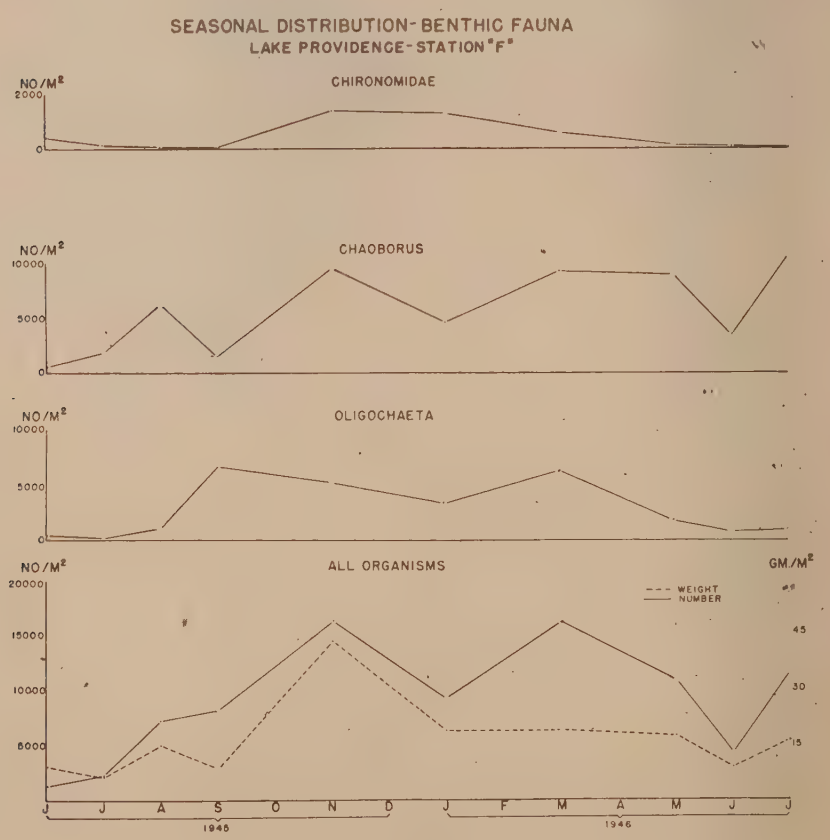

FIG. 4. Annual cycle of profundal bottom fauna, Station "F".

spring, when a gradual decline in numbers occurred.

The population curve for Chironomidae shows a progressive decline from June 28 through September 27, 1945, on which latter date no specimens were collected. Station "F" was still thermally stratified on September 27, with complete oxygen exhaustion in the lower hypolimnion. This population decline may be attributed, in part at least, to the prolonged period of anaerobiosis (over 100 days) to which the profundal benthos at this station were subjected.[4] A rapid increase in the profundal chironomid population of Lake Providence took place in October and November, probably as a consequence of the reinauguration of water circulation following the fall overturn. The maximum population was maintained until January, 1946, followed by a gradual and progressive decline in numbers throughout the spring and summer.

The seasonal population curves for Chaoborus and Oligochaeta conformed to the general form of the chironomid curve, but there were certain striking differences. Most apparent, perhaps, was the summer increase in Chaoborus noted in both August, 1945 and July, 1946. This consisted for the most part of very small individuals and undoubtedly represented recently hatched larvae from eggs deposited the same summer (cf. Lindeman, '42b, pp. 440–442). Further, it might be expected that the habit of diurnal vertical migration characteristic of Chaoborus larvae (Eggleton, '32) would render the prolonged anaerobic conditions of the profundal zone less destructive of them than of the Chironomids which are restricted to the bottom mud.

More puzzling is the mid-winter drop in population density in January, 1946 affecting both the Oligochaeta and Chaoborus. Both forms were restored to nearly their former numbers at the time of the next visit (March, 1946), suggesting that the apparent population decline might be simply a sampling error. If so, it is difficult to see why the same error was not reflected in the chironomid population on the same date.

[4] In this connection, Lindeman ('42a) has shown that experimentally controlled anaerobic cultures of Chironomidae, Chaoborus, and Tubificidae survived for shorter periods relatively unharmed, but that nearly complete mortality occurred in anaerobic cultures maintained at 10° C for 90 to 120 days.

Fish Mortality

At no time within the period June, 1945 through September, 1946 during which the lake was under regular observation was any notable fish mortality observed or reported. The writer had been informed that for several years previous to 1945 (apparently since the elimination of the Wilson's Point area from the drainage basin of Lake Providence in 1933) such mortality had been an annual occurrence. Reports of local residents concurred in assigning the time of such mortality to September or October; commonly the kill took place in the early morning, after a day or more of cold rain.

On the basis of these reports it seemed probable that the fish mortality was caused by dissolved oxygen deficiencies in localized areas resulting from the respiratory activity of an excessive phytoplankton population, or from the death and decomposition of a considerable proportion of the phytoplankton.

More than a year after the regular schedule of visits had been terminated, a fish-kill was reported at Lake Providence. The mortality occurred during the early morning hours of October 15, 1947; due to delay in transmitting the report and the distance of the lake from New Orleans, the writer did not arrive at the site until the evening of October 17. The lake level at this time was about one foot lower than had been recorded at any time during the previous twenty-eight months, and was far below the crests of the concentration dams. This was probably attributable to a precipitation deficiency of 4.24 inches during the previous summer, about 26% below normal.

The mortality involved chiefly small gizzard shad and bream; the dead fish were observed along nearly a mile of shore line in the southwest corner of the basin. Counts were made and it was estimated that approximately 100,000 shad had been killed of which only about 10% were over four inches in length. An estimated 15,000 bream were noted, of which about 60% were less than three inches long. Small numbers of largemouth black bass, white crappie, and sheepshead were also observed, as well as numerous top minnows, silversides, and other small species. No rough fish or gar were involved.

Although nothing is known of the phytoplankton of the lake during the summer of 1947, the bright green color of the water at the time of the October visit and the typical "algae" odor, noticeable as soon as one approached the lake, testified as to its former abundance. Water temperatures taken at a three meter station at the south end of the lake, the region in which the fish mortality had presumably occurred, showed a difference of only 0.5° C between surface and bottom. Despite the absence of any thermal stratification, the lower levels exhibited complete absence of dissolved oxygen although the surface waters were about 75% saturated.

This evidence was interpreted to mean that active bacterial decomposition, probably associated with the death and subsequent sinking of a large proportion of the plankton algae population, had occurred in the lower strata. Wind velocity and wave action had been very slight for several days preceding the fish-kill, and water circulation was at a minimum. It seems probable that the postsummer death of a considerable amount of the phytoplankton resulted in temporary (and local) conditions of reduced oxygen tensions which was the immediate cause of death of the more delicate shad and bream. Apparently the oxygen depletion was not severe enough on this occasion to affect adversely the more tolerant species of game and rough fish, or even the majority of the larger individuals of the two species named.

Summary

1. Lake Providence, in East Carroll Parish, Louisiana, has an area of approximately 1,380 acres and a maximum depth of forty feet. It is supplied mainly by run-off, and seepage from the nearby Mississippi River; it drains through two outlets on the west side of the basin.

2. The lake exhibits one usually continuous period of thermal stratification from May or June through September; followed by a period of continuous water circulation from October through April. Surface and bottom temperatures display marked annual fluctuations, although they apparently never fall below 4° C.

3. The period of thermal stratification is characterized by high dissolved oxygen tensions in the epilimnion, frequently exceeding saturation. At the same time marked oxygen deficiencies, including conditions of complete exhaustion, are characteristic of the lower thermocline and hypolimnion. There is a complete absence of any winter stagnation period.

4. Lake Providence is a "hard-water" or "high carbonate" lake, a type usually characterized by abundant aquatic vegetation and high productivity of animal life. In the present instance the plant life is composed chiefly of phytoplankton.

5. The surface plankton is composed principally of blue-green algae (Myxophyceae), especially Chroococcus, Anabaena, and Lyngbya. Chlorophyceae and Bacillareae are quantitatively of much less importance. Zooplankton is relatively scanty, the predominate group being the Rotifera.

6. Productivity in terms of benthos is high, the "summer standing crop" averaging 90.4 pounds per acre (drained wet weight). The sublittoral zone is most productive, the littoral zone shows the greatest diversity of types, while the profundal benthos is practically limited to

three forms: Chironomidae, Chaoborus, and Oligochaeta.

7. With reference to the possible causes of late summer fish mortality at Lake Providence, it would appear that the dense population of blue-green algae is responsible. Such mortality might be occasioned by excessive respiratory activity of the algae, by oxygen depletion due to decomposition, or by a combination of the two.

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COMPARATIVE METABOLISM OF ORGANIC DETRITUS BY INSHORE ANIMALS *

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In any area of biological productivity, the total quantity of unorganized, raw material must considerably exceed the mass of organized living matter. Thus, in different inshore marine areas, we may expect to encounter such numbers and varieties of living animal species as will reflect not only those physical conditions which favor successful harborage, but continuous supplies of raw food materials as well. Rich zones of varied and perennial faunal productivity will be observed in foreshores which are characterized by water of moderate temperatures and freedom from protracted violent impact with the shore. In addition, the presence of gradual slopes, leading up to varied substrates of stationary rocky structures and to sandy beach areas, affords adequate surface for colonization by numerous sedentary forms, and various kinds of refuge for many migratory species. Maximal colonization will be favored by the transport of terrestrial detritus to such areas by rivers, streams or rainfall run-off. Such permanent or seasonal tributaries will contribute valuable raw materials of various kinds, whether in the form of plant nutrient salts or organic detritus commonly associated with humus (Sverdrup, Johnson and Fleming, '42).

This brings us to a brief consideration of the sources, character and disposition of marine detrital organic matter. In the first place, it is derived from the decomposing bodies and dead gametes of countless plants and animals from the largest to the most minute, from the excrement of animals and, at certain regions, from sewage, industrial wastes and other materials of terrestrial origin (ZoBell, '46).

Much discussion has in the past been devoted to the nutritive value of so-called "soluble" organic matter for marine and other aquatic animals. Controversial viewpoints surrounding this question would seem to call for discriminating definition of what is meant by solubility. There is no doubt that many aquatic animals subsist largely upon organic materials which are present in various stages of fine subdivision, including considerable amounts of molecular aggregates of such minute size as to be microscopically invisible. But these entities, if they exceed 1 mμ in mean diameter or in the longest dimension, are not to be classified as soluble in the true chemical sense, i.e., as molecularly dispersed solutes in the sense which applies to many inorganic salts, amino acids, sugars, etc. Rather, they exist in the colloidal state, sometimes referred to in ordinary parlance as in colloidal "solution," or in that imperfectly defined realm of sizes lying between 1 mμ and 0.1 μ in mean diameter. Such submicroscopic micelles are visible only in the ultramicroscope, save when coagulated or precipitated into larger aggregates. Dispersed in aqueous media, these biocolloids are readily adsorbed to solid surfaces such as rock, sand or wood, or to hydrophilic substances such as the mucus sheets, cilia and fine sieves which characterize the feeding apparatus of many marine animals.

Marine organic detritus exists in relatively large masses, in coarsely particulate form, and in various grades of colloidal dispersion, with all intergrading sizes represented. Such small quantities of truly soluble organic matter as may be present are in all probability relatively negligible

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from the standpoint of their direct usefulness to animals, since, in typical cells or body fluids which serve as the source of marine organic materials, some 98% or more of the raw organic substance exists in colloidal or even coarser states, e.g., membranes, fibers, droplets, etc. While marine bacteria which actively decompose masses of organic material certainly hydrolyze protein, lipid and carbohydrate to yield smaller, soluble molecules, these same bacteria are of the sessile or sedentary type, adhering closely to the surface of the material which they are digesting. Prompt and efficient assimilation of the soluble products generated by extracellular digestion of the substrate makes possible the survival and multiplication of the attached bacterial consumers (ZoBell, '46).

Being chiefly of a hydrophilic character, and carrying negative micellar charges, considerable quantities of colloidal organic detritus are to be found suspended in near-shore waters. The property of "stickiness" or adhesiveness permits their adsorption to submerged marine surfaces such as those mentioned above. Alternatively, large quantities of the material may be precipitated to the bottom by salt-flocculation, by coacervation with other colloids, or by mutual neutralization of electric charges afforded by still other micelles, often of an inorganic nature.

Due to the described conditions which apply to many inshore areas, the magnitude and variety of animal populations are maximal in such regions, and the quantities of organic matter utilizable by them likewise achieve the greatest concentrations in suspended, adsorbed and precipitated form. The value of 5 mg of "dissolved" organic matter per liter of near-shore ocean water, estimated by Krogh and by ZoBell ('46), is doubtless a conservative one, since adsorbed and suspended colloidal material, as well as coarser aggregates, must obviously contribute very substantially to conditions.

It is suggested that some such term as *emulsoid* or *suspended* be substituted for the unsatisfactory word "soluble" as applied to the dispersed organic matter in marine waters. Even were certain aquatic animals to depend upon true organic solutes for a substantial part of their nutrition, the extremely low concentrations of such molecules in surrounding waters would appear to impose the necessity for an enormous output of energy in the form of osmotic work and maintenance, not to mention the complexity and efficiency of the nephritic or other excretory apparatus which would be requisite for handling the vast quantities of water involved.

In addition to readily utilizable compounds such as proteins, certain lipids and hydrolyzable polysaccharides, e.g., starch and glycogen from ruptured cells, numerous relatively inert substances contribute to the organic detritus of the sea. Some of these are cellulose, keratins, chitin, sterols, pigments and the like. The more refractory colloidal members of the complex organic substrate are rendered into cell constituents and molecular by-products by marine bacterial flora of the water and bottom, and are later returned in another form to the general biochemical cycle (fig. 1).

Omitting from the present discussion exclusively carnivorous animals and those others which feed predominantly upon living plant material, we are concerned here chiefly with the numerous species which depend upon the copious supplies of finely divided and suspended, adsorbed or precipitated organic detritus as a primary source of nutrition. While the species of detritus-feeders are many and varied, they have been divided, for the purposes of this discussion, into three main groups, some members of which practise two or more feeding habits as follows:

1. Animals which filter out colloidal and other finely particulate detritus by means of cilia and mucus-covered sieve or net structures. Examples are to be found in the sponges and tunicates, in all or the great majority of lamellibranch mollusks, among the crinoids and among

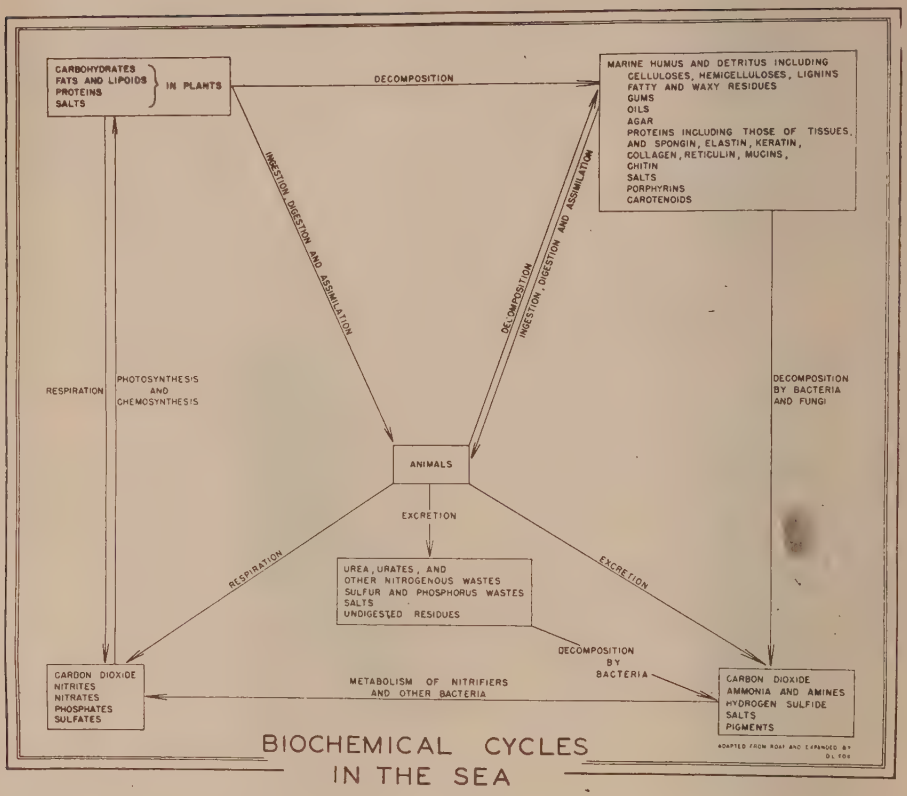

FIG. 1

sabellid, echiuroid and certain other worms (Coe, '45, '47, '48; Coe and Fox, '42, '44; Fox and Coe, '43; Scheer, '48; Yonge, '36).

2 Animals which graze upon the ocean floor, either (a) utilizing tentacles, arms or similar structures for gathering sapropel (finely precipitated loose organic material on the mud-surface), or (b) sucking in and swallowing whole mud or sand with the use of a muscular pharynx. Among the grazers are ophiuroid, holothurian and crinoid echinoderms and certain crustaceans, while species which swallow whole sand, mud and other included detritus are represented by numerous sipunculid and annelid worms (Yonge, '36; Fox and Scheer, '41).

3. Animals which feed by scraping adherent material from rocks, shells, pilings and other submerged surfaces. Limpets and other gastropods which, with their file-like radulae, typify this habit, swallow organic slime with its included bacteria, sessile algal cells and animal materials (Yonge, '36).

As pointed out by Yonge and confirmed by studies at the Scripps Institution, such animals as bivalved mollusks, which subsist upon finely particulate marine materials, may characteristically possess copious amounts of amylase and glycogenase as extra-cellular secretions in the alimentary tract, e.g., in the so-called "crystalline" style, a long, rod-shaped non-cellular structure extending for the length of a special sac which lies in open communication with the lumen of the gut. On the other hand, such detritus-feeders secrete but insignificant amounts, if any

at all, of proteolytic enzymes. Nor are lipoclastic enzymes found free in the gut in appreciable amounts. Protein and fat are therefore digested intracellularly in such species, i.e., following engulfment by special cells of the digestive gland or by wandering phagocytes. Extra-cellular proteases are to be found in copious amounts in carnivorous species such as coelenterates, asteroids and cephalopods, which are incapable of deriving nutrition from plant material.

Although there are similarities in the general nutritive and metabolic habits of detritus feeders, there are also interesting differences in the manner in which certain known molecules are handled by the consumers. Among the many classes of organic molecules associated with suspended matter in the sea, there are some which lend themselves readily to chemical isolation and identification. Such compounds are consequently of value in diagnosing general biological conditions in selected marine localities. The chlorophylls of marine phytoplankton, or these accompanied by greenish degradation products of chlorophylls in muds, in feces, and in water areas of dying plant populations, are frequently measured as approximate indices of plant activities. Similarly, approximate concentrations of the fat-soluble yellow, orange or red carotenoids may be measured instead or in addition. For these lipochromes characterize all green plants, many saprophytes and most animals, the latter deriving the pigments directly or indirectly from plants. Furthermore, the carotenoids generally maintain their molecular integrity for longer periods than do chlorophylls. Thus they may pass through the alimentary tracts of numerous plant- or detritus-eaters without usually undergoing the degradation which chlorophyll does. As a result, carotenoids may often be recovered from detrital materials which yield no chlorophylls as such, and but relatively small quantities of greenish chlorophyll breakdown products (Fox, Updegraff and Novelli, '44).

The subject of marine biochromes has been introduced here because such compounds have proved to be useful in comparative biochemical studies of marine animals, and because investigations of the same pigmentary compounds in marine muds have thrown some light on metabolic chapters of past decades and centuries. The great majority of marine animals investigated to date selectively assimilate and store the xanthophyllic or alcoholic type rather than the carotene or hydrocarbon class of carotenoid. This does not apply to all marine fauna, as will be seen, but seems to be true especially of carnivorous forms, including many fishes, and of numerous herbivores and omnivores, whose tissues may yield solely or chiefly xanthophylls (Fox, '47).

There are, however, some interesting differences among detritus eaters with regard to their carotenoid metabolism. Certain sponges, for example, have been found to exhibit a preponderance of carotenes over xanthophylls, while some of the tunicates assimilate substantial quantities of both types of lipochrome. Numerous lamellibranch mollusks store in their gonads, digestive gland and other tissues only members of the xanthophyll class; this is notably true of the California mussel. The bottom-feeding holothurian, *Stichopus californicus,* yields very small but approximately equal quantities of both carotenes and xanthophylls. Three ophiuroid species studied contained no carotenes at all, but relatively rich supplies of unique esterified xanthophylls. Several bottom-eating echinoid species yield both carotenes and xanthophylls, the former preponderating. The bottom-grazing asteroid *Astropecten californicus* yields many fold the quantities of xanthrophyllic compounds as it contains carotenes (Fox and Scheer, '41). The beach annelid worm *Thoracophelia mucronata,* subsisting on a basic diet similar to that consumed by the other animals cited, assimilates from this mixture only β-carotene, seemingly eliminating α-caro-

tene and largely destroying ingested xanthophylls in the gut (Fox, Crane and McConnaughey, '48).

The foregoing examples are illustrative of the different manner and degree to which various detritus consumers may dispose of ingested carotenoids, and may materially alter the ratio of xanthophylls to carotene members as these occur in the sea. The metabolic habit of assimilating xanthophylls, or of partially destroying them by biological oxidation, and of rejecting carotenes, would appear to be a salient factor in effecting the arresting reversal in ratio of xanthophylls to carotenes observed in muds from the ocean floor. Phytoplankton and suspended material, collectively filtered from sea water by artificial devices or by the efficient mechanism possessed by the mussel, for example, characteristically yield xanthophylls and carotenes in ratios of about 9:1. As might be expected, the same general proportions hold for the carotenoids extracted from wave-washed beach sand. But at greater depths in the ocean, the mud surface, yielding lower quantities of total carotenoids, contains greater proportions of carotenes than xanthophylls. At levels beneath the mud surface, from a few inches to several feet, at water depths of 100 fathoms or more for example, carotenes may constitute 80% or more of the total carotenoids. The fact that several bacterial carotenes are encountered in marine mud cores, but that the common crustacean xanthophyll astaxanthin is rarely if ever detected,

TABLE I. *Turnover of water, inert material and organic matter by mussel,* Mytilus californianus 1,000,000 animals from age 1 year to age 2 years

	Age 1 year	Age 2 years	Increment
Total weight	51.2 tons	117.6 tons	66.4 tons
Dry weight tissues	2.3 tons	6.4 tons	4.1 tons
Weight shell	26.0 tons	77.7 tons	51.7 tons
Minimal quantity of water filtered per year (22,000 l. per mussel)			22,000,000 tons
Minimal quantity of organic matter removed from water per year (5 mg. per liter)*			121 tons*
Inert materials filtered from water			ca. 400 tons
Approximate efficiency (*maximal*) $\frac{4.1}{121} \times 100 =$			3.3%**

* Conservative figures; probably too low.
** Probably excessive by 2 or 3-fold.

TABLE II. *Turnover of sand and organic matter by beach worm,* Thoracophelia mucronata

(See plates I and II)

Volume of sand in worm-bed 1 mile long, 10 ft. wide, 1 ft. deep	52,800 cu. ft.
Weight of (dry) sand in this volume	2,820 tons
Total number of worms in worm-bed (ca. 3,000/cu. ft.)	158,000,000
Weight of worms in worm-bed (ca. 0.04 g. each)	7 tons
Weight of sand cycled annually by worms (ca. 84 g. each)	14,600 tons
Ratio of sand cycled annually to sand in worm-bed $\frac{14,600}{2,820} =$ (equivalent to all sand in the bed once every ten weeks)	5.2
Organic matter in sand cycled annually by worms (ca. 1%)	146 tons
Organic matter in worms of the whole colony (ca. 20%)	1.4 tons
Relative efficiency of worms, maintaining a standing population, assuming an annual life-cycle: $\frac{1.4}{146} \times 100 =$	0.96%
Volume of sand on La Jolla Shores beach (wedge 1 mile long, 200 ft. wide, 2.5 ft. high)	1,320,000 cu. ft.
Weight of this sand	70,500 tons
Fraction of sand on beach cycled annually by worms $\frac{14,600}{70,500} \times 100 =$	21%

PLATE I. Bed of *Thoracophelia mucronata* (darker area in foreground, outlined) on S. I. O. beach.

would lead one to suspect that bacterial flora of the ocean floor may play a role in destroying or chemically reducing xanthophylls.

The right quadrant of the chart (fig. 1) indicates the primary region of discourse in the present contribution. Tables I and II indicate the respective activities of two representative detritus consumers: the mussel, *Mytilus californianus,* each medium-sized specimen of which filters a minimum of 110 grams of organic detri-

Plate II. *Thoracophelia mucronata* (beach worm); close view of colonies on S. I. O. beach.

tus, and several times this quantity of sand, silt and other inert material, from some 22,000 liters of water annually (Fox and Coe, '43); and the beach worm, *Thoracophelia mucronata,* each 40 mg. individual of which cycles annually through its gut a minimum of 84 grams of sand containing about 1% of organic matter (Fox, Crane and McConnaughey, '48).

The photographs (plates I and II) show the beach-excavating activities of the sand-swallowing worm, which occurs in enormous numbers.

It should be emphasized that the mussel does not gain sufficient nutrition from the large numbers of diatoms and dinoflagellates swallowed. These phytoplankton are not present in sufficient numbers to balance the mussel's nutritional budget as determined experimentally by the annual increase of its organic matter (Fox and Coe, '43). Furthermore, dinoflagellates and diatoms, ingested while living, pass through the alimentary tract unchanged in great numbers, and have been successfully cultured from fecal straps removed in an uncontaminated condition from the rectum and placed in nutrient sea water (Coe, '45). The mussel carries no effective cellulase for the digestion of the cellulose envelope possessed by many dinoflagellates (Coe, '45, '47). Nor does the worm *Thoracophelia* subsist upon whole organisms. Its gut contents reveal no recognizable ingested cells, save for a very few minute sessile algae attached firmly to the ingested sand grains. These algal cells appear to be as numerous upon fecal sand voided by the worms as upon the sand before ingestion.

These detritus-consuming animals and their countless allies of similar nutritional habit, at work in inshore regions, especially near river-mouths or other localities of copious run-off, must undoubtedly alter the physical and chemical nature of both the water and the bottom, not only at the site of operations, but also at considerable distances out from shore.

Summary

1. The sizes of populations which will be supported in a marine inshore area are dependent upon the quantities of organic detritus which may serve as food, either directly or by contributing to the total carbon budget.

2. Great numbers of marine invertebrates feed primarily upon organic detritus. They obtain it by (1) filtering such colloidal or other finely particulate material from the water, (2) swallowing whole mud, sand and other inert material to which the organic matter is adsorbed, or (3) scraping it from extensive immersed surfaces.

3. Biochromes, such as red, orange or yellow carotenoids or greenish breakdown products of chlorophyll, provide valuable means of studying the comparative biochemistry of nutrition and assimilation, especially as derived from suspended or precipitated detrital materials.

4. While xanthophyllic carotenoids preponderate greatly over carotenes in fresh, suspended plankton and detritus and in numerous detritus eaters, carotenes are the predominating carotenoids of buried marine muds, and of a few detritophagous animals.

5. Comparisons are drawn between two typical marine detritus feeders: (a) mussels, which filter vast quantities of water annually, removing therefrom the finally suspended organic matter from which some of the xanthophylls are assimilated and the carotenes quantitatively rejected, and (b) the beach-annelid, *Thoracophelia,* colonies of which cycle tons of sand annually through the alimentary tract, gaining nutrition from the adsorbed film of colloidal organic matter, from which β-carotene is selectively assimilated, while xanthophylls are rejected and largely destroyed.

6. Such biological agents and their countless allies alter the chemical and physical nature of both water and floor, not only near the coast but at considerable distances out from shore.

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THE PROBLEM OF PHYSIOLOGICAL SPECIES WITH SPECIAL REFERENCE TO OYSTERS AND OYSTER DRILLS

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INTRODUCTION

The term physiological species, as used here, is meant to describe those groups of organisms which, on morphological grounds, fit a presently accepted species designation but which are functionally different in certain respects one from the other. Many other terms have also been used in dealing with such groups of organisms including biological races, varieties and strains (see Bates, '40). Some examples from other fields will not only illustrate the idea but suggest the practical importance which may result from a recognition of their existence. A species of parasitic roundworm from the chimpanzee is morphologically indistinguishable from *Ascaris lumbricoides* found in man or in the pig, yet the strain found in the chimpanzee is specific for that host and not infective for the other host species (Augustine, '39). The strains in man and the pig are also each specific for these hosts (Faust, '39). This discounts the importance of the pig as a reservoir host in the control of human ascariasis.

Anopheles maculipennis was described in 1818 by Meigen. It was over 100 years later, however, when Bates ('40) wrote that this so-called species forms "a group of more or less independent populations distinguished by various physiological and morphological characters." The physiological characters include (1) different tolerances of the larvae for sea water, (2) variations in adult sexual and feeding behavior, (3) sterility of F_1 hybrid males and (4) differences in ecological and geographical distribution (Bates and Hackett, '39). Some 20 latinized names have been proposed for these groups and Bates himself recognizes 6 distinct species although the only important morphological differences are in egg pattern and structure, *not in adult form.* Yet the recognition of these distinct types has solved many vexing problems of the epidemiology of malaria in Europe.

The races "A" and "B" of *Drosophila pseudoobscura* are another example. "These 'races' have distinctive geographical distributions that, however, broadly overlap without the formation of hybrids in nature. The ecological preferences are somewhat different; a pronounced, though incomplete, sexual isolation is observed; the F_1 hybrid males are absolutely sterile; and the viability of the backcross products is decreased" (Dobzhansky, '41). In short, these races are "distinct species by any criterion except the absence of morphological differentials" (Mather and Dobzhansky, '39).

That similar examples exist among inshore marine invertebrates is especially plausible to those who know the striking morphological and physiological differences between oysters of the *edulis* and *virginica* types still classified in the same genus despite these great differences (Orton '28; McLean '41). The presence of physiological species could also explain Mayer's observations in 1914 on the different effects of temperature on bell rhythm in *Aurelia aurita* from Halifax and from Tortugas. Furthermore, Runnström ('29, '36), who has devoted much thought and effort to this problem in European waters, has concluded that physiological races of several marine invertebrates exist in the Eastern Atlantic.

Without attempting to enter the discussion of what a species is, Dobzhansky's ('35) dynamic definition seems most useful in this connection. He defines a species as "that stage of evolutionary process

at which the once actually or potentially interbreeding array of forms becomes segragated into two or more separate arrays which are physiologically incapable of interbreeding." Here the species is a stage in a process and not necessarily a static unit. The concept emphasizes the role of physiological isolation as a factor in speciation and what populations of organisms do in nature as opposed to what might be accomplished with them under laboratory experimentation.

Hutchins, in a most excellent address two years ago, described the bases for temperature zonation in the geographical distribution of marine organisms (Hutchins, '47). His main points were that the north-south zonal boundaries of organisms are to be interpreted in terms of summer and winter temperatures critical for repopulation or survival and that "four basic types of zonation can be recognized each having a distinctive combination of summer or winter boundaries for its poleward or equator-ward limits." He has shown how the zones of the four types have distinctive configurations around the world depending on differences in distribution of summer and winter temperatures and how these may be used to explain effectively the geographically distinctive distributions of organisms.

According to McLean ('41) it is impractical to try to give exact geographical ranges to the various species of oysters because of the divergent opinions on suitable characteristics and of the uncertainty of identification in this group. However, he indicates that *Ostrea virginica* ranges from Prince Edward Island, Canada, at least as far south as Rio de Janeiro, Brazil. Although McLean disclaims the uniquenes of such a great range of distribution for an organism, in terms of Hutchins' report *O. virginica* straddles at least three of the important change points on the North Atlantic coast (Cape Cod, Cape Hatteras and Palm Beach) and the equator as well. While Hutchins did not deal specifically with the oyster, the extension of *O. virginica* across the equator constitutes a type of zonation without an equatorward temperature limit for either survival or repopulation. Hutchins has given theoretical consideration to such distributions though, practically speaking, the oyster would not fit any of his four basic types.

Furthermore, Hutchins has not touched upon the subject matter of this presentation; namely, that within the range of such a given species as *O. virginica,* arrays of physiological varieties may occur whose critical temperatures differ and whose separate distributions, perhaps even overlapping one another, add up to the total observed distribution of the morphological species. (See Runnstrom, '29, '36.)

The concept of physiological species is not a new one, even with reference to the oyster (Nelson, '47), but data are still scanty and therefore it is hoped that this presentation will be a stimulus for the further work which is so obviously needed.

It should be clearly understood that my role in this field has been a minor one, that most of the actual data to be discussed are the results of the long-term efforts of others. I am especially indebted to Dr. T. C. Nelson, who 18 years ago first suggested to me the possibility that physiological varieties of the oyster might exist and who has contributed so much valuable information as well as the stimulus for these studies and to Dr. P. S. Galtsoff, who made available for examination the unpublished records for several areas studied by himself and his associates.

The Oyster

It is important to note that, prior to 1931, for both the waters of Prince Edward Island, Canada, and of various parts of the United States various authors stated 20° C to be the water temperature at which spawning was initiated in *O. virginica* under field conditions (see Nelson, '28, and '28a, for a summary of

these observations). The most extensive data are for the waters of Barnegat Bay where observations were made by Dr. Julius Nelson and Dr. T. C. Nelson for almost 50 consecutive years. For over a decade these observations included water temperatures automatically recorded by a continuously recording thermograph. From this body of data the essential relationships between water temperature and the spawning of oysters on the oyster beds were firmly established and have been amply confirmed. These relationships may be stated simply as follows: On an oyster bed with the gradual rise of water temperatures in the spring of the year oysters begin to feed, grow and become sexually ripe but that there is a minimum temperature requirement for the initiation of the act of spawning. Although spawning is a group reaction, not all oysters spawn when this level is reached and some will spawn experimentally at lower temperatures and under other special laboratory conditions. There may even be some oysters which naturally deviate from this minimum level especially under unusually rapid temperature rises but the year after year picture for a carefully studied body of water is essentially the same—no spawning until the minimum temperature is reached and then mass spawning of a significant proportion of the oysters on the bed. Subsequent spawnings may occur at higher than the minimal temperature but in the autumn again after temperatures fall below the observed minimum no further spawning is noted.

The kinds of data used to draw such conclusions are gathered by observing the meats of the oysters themselves either in the gross or in section (Loosanoff and Engle) by examination of water samples for the distinctive larval stages of the oyster with their known cycle of development (J. Nelson and many others) or by the collection of recently attached young oysters set on clean shells regularly exposed, removed and examined. All methods give significant data but, for any one area, one or more of the methods may be easier to apply especially when dealing with large bodies of water and widely scattered areas of oyster bottom.

The words "minimum spawning temperature," "spawning temperature" and "critical temperature for spawning" have not all been used to designate the same stage in the phenomenon. While the differences in meaning are important to a full understanding of the spawning reaction they probably are of lesser consequence in the present discussion. Therefore, though all spawning temperatures may not be directly comparable, nevertheless, the differences between the spawning temperatures reported are believed to be significant.

The first published evidence that not all oysters in the geographical range of *O. virginica* spawn at a minimum level of 20° C is that of Hopkins in 1931. Reporting for Galveston Bay, Texas, he found that spawning did not start until 25° C was reached and that when 20° C was reached the oysters were just beginning to develop mature eggs and sperms. Loosanoff ('32) reported similar findings for the James River. The next deviation reported was that of Loosanoff and Engle in 1940, who claim a minimum spawning temperature of 16.4° C for Long Island Sound. It should be noted, however, that an unpublished deviation had been observed elsewhere. When Dr. T. C. Nelson shifted the scene of his activity from Barnegat Bay to Delaware Bay, N. J., in the late twenties he soon learned that spawning phenomena were not the same in these two locations. Indeed, on several occasions he noted that spawning and setting might occur in Barnegat Bay before spawning had begun in Delaware Bay although the latter was farther south and warmed up at least equally as rapidly. Subsequently the findings of Dr. Nelson, Mr. J. Richards Nelson and myself over the following decade and a half amply support, I believe, the contention that mass spawning of oysters over the larger beds of oysters in Delaware Bay does not

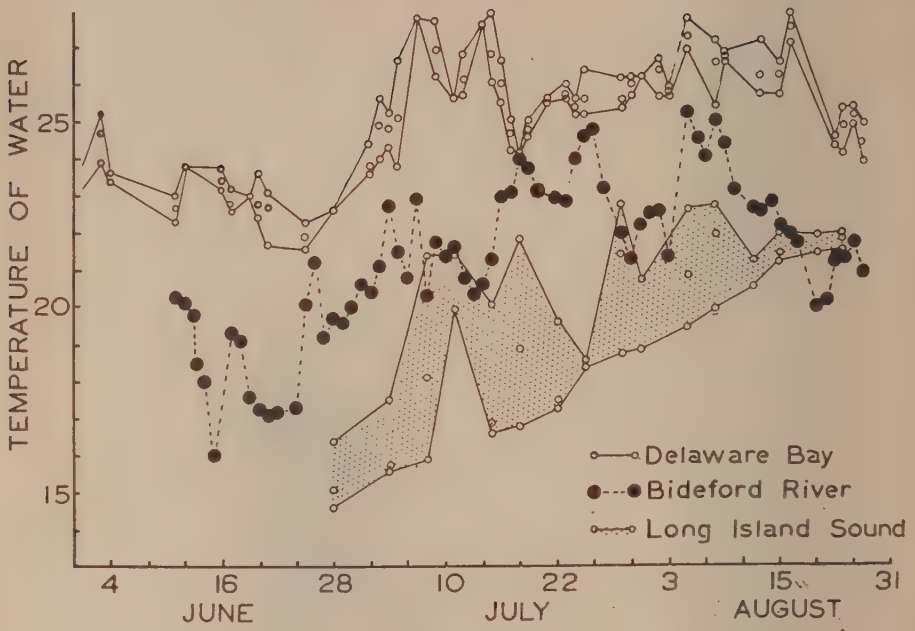

FIG. 1. Water temperatures in the late spring and summer of 1937 in Delaware Bay, Bideford River, Prince Edward Island, Canada (Medcoff, '39) and Long Island Sound (Loosanoff and Engle, '40). Only bottom temperatures are plotted. For Delaware Bay the extremes of the daily samplings of several stations are plotted; for Bideford River the daily samplings at one station; and for Long Island Sound the approximately weekly samplings at 3 representative stations in 10, 30 and 60 feet of water.

occur until water temperatures reach 25° C. (I think we must exclude the very shallow inshore areas from consideration because of the greater amplitude of the temperature fluctuations noted in them, though we should note Chestnut's ('48) belief that spawning in one inshore area of Delaware Bay is observed at 22.5° C. The important point is that it is not 20° C.)

It might then be stated that at least three types of oysters exist on the Atlantic seaboard each of which shows a different minimum spawning temperature. The great problem in accepting this viewpoint was the apparent difficulty of reconciling the 20° C minimum spawning temperature of the oysters of Eastern Canada with that of a lower minimum spawning temperature for Long Island Sound, geographically some 600 miles airline to the Southwest. Certain data for the year 1937 presented the opportunity for resolving this problem. On figure 1 are plotted the published data of Loosanoff and Engle ('40) for bottom water temperatures at three stations in Long Island Sound off Stratford Point in 10, 30 and 60 feet of water during the summer of 1937. Also plotted are the published findings of Medcoff ('39) for the same year ('37) for the waters of Bideford River, Prince Edward Island, Canada, and our own unpublished records for several scattered stations in the New Jersey waters of Delaware Bay. It is immediately evident from this figure that little overlapping of temperatures occurs in the three areas and that they fall in the sequence of the minimal spawning temperatures of 25°, 20° and 16.4° C reported, with the Bideford River falling between those of the other two, though geographically so much farther north.

It might be claimed, however, since all three areas do reach 20° C at some time in the summer, that the same 20° C temperature could conceivably initiate spawning in each area. For Delaware Bay the water temperature was maintained above 20° C after May 24, 1937, in Bideford River after June 30, but in Long Island Sound at least not until after July 12 or a spread of no less than 48 days for the three areas. The times given by the observers for the first *general* spawning in the areas mentioned, however (excluding minor spawning of inshore areas), are July 7–8 for Delaware Bay, June 26–30 for Bideford River and July 3 for Long Island Sound, a spread of only 12 days for such widely separated areas. This general agreement in time of initial spawning in the three areas when temperature conditions were so markedly different, is a very likely indication of the presence of three physiological varieties of oysters with different minimum spawning temperatures, most probably the 25°, 20° and 16.4° C values already mentioned.

Let us look at the problem in another way. For Barnegat Bay in 1933 there were 18 weeks above the minimum spawning level of 20° C and 9 weeks each in spring and autumn between 5° and 20° C (T. C. Nelson, unpublished). If these intervals represent a favorable balance between periods for growth and for reproduction in the oyster on the natural oyster beds and if the 20° C spawning level were the limiting factor throughout the range of the species *O. virginica,* then oysters in some areas might not have persisted in their respective localities. Whereas in Texas there are 33 weeks with temperatures above 20° C, in Long Island Sound there are less than 9 weeks above 20° C, and because of prolonged winter inactivity or reduced opportunities for spawning the species might have been eliminated. Many investigators already believe that the great masses of oyster shells in the kitchen middens of Maine can best be explained in such a fashion by the failure of favorable spawning conditions to occur, probably due to a combination of climatic conditions plus the depredations of man.

Table I illustrates this point in another way showing the water temperatures observed in several oyster-growing waters of eastern North America. Actually Delaware Bay seems to be the borderline between more northerly areas with brief or no periods of water temperatures above 25° C and more southerly areas with few or no consistent temperatures below 5° C. Obviously, conditions along the seacoast from Long Island Sound to Texas are so different that the assumption of biological varieties of the oyster would make more reasonable the observed distribution of the oyster since it would make possible combinations of periods of growth and reproduction more likely to

TABLE I. *Inshore water temperatures, eastern and southern North America*

Locality and reference	Temperatures—approx. weeks of duration		
	Above 25° C	Above 20° C	Below 5° C
Prince Edward Island (Medcoff)	0	6–8	28
Long Island Sound (Loosanoff & Engle) (Riley)	0	8–9	13
Barnegat Bay (Nelson)	3 (not continuous)	15–18	14
Delaware Bay (Stauber)	6	17	15
Middle Chesapeake (Md.) (Newcombe) (Beaven)	1–7	17–21	4
Lower Chesapeake (Va.) (Federighi) (Galtsoff *et al.*)	9	22–24	1–9
Beaufort, S. C. (Smith)	19–21	29	0
Apalachicola, Fla. (Pearse) (Smith)	19–21	29	0
Louisiana (Kavanagh) (Owen)	18	29	0
Texas (Moore) (Hopkins)	27	33	0

The author is greatly indebted to the above mentioned investigators for the use of their largely unpublished data.

be consistent with the survival of the species. Runnstrom ('29, '36) has come to similar conclusions for European waters but Hutchins ('47) has shown how much greater the temperature changes are in the West Atlantic, making important change points relatively close geographically. However, it must be noted that for any given morphological species there are extremes beyond which no further such combinations are possible. One of these for the oyster is 5° C, the approximate temperature at which ciliary activity (Nelson, '26; Galtsoff, '26), shell movements and heart beat (Stauber, unpublished) cease. The other is in the neighborhood of 33° C, very nearly the upper limit of water temperatures on continuously water-covered oyster beds in the United States. Within these limitations the evidence seems to indicate three varieties of *O. virginica.*

Geographical isolation is recognized by biologists as an important factor in the origin of new species. The degree of isolation was recently emphasized by Fleming (unpublished) as an important feature to be included in a classification of inshore environments. For the thousands of years before the white man began to shift oysters from bay to bay on our seaboard, the degree of isolation of the oysters of Delaware, Barnegat and Chesapeake Bays and Long Island Sound was practically complete. The oyster, as we know it, is not an ocean but an estuarine dweller, so it is extremely difficult to conceive that interbreeding at the margins of the group areas could have occurred in recent time. Assuming that mutation occurs in oysters as in other forms of life, the existing geographical isolation and the geologic time available would have been favorable for the action of natural selection and the production of biological species of the oyster.

If these physiological varieties are as real as they seem to be there are a number of practical implications for the oyster industry. Suppose, for example, oysters from Chesapeake Bay with a probable minimum spawning temperature of 25° C are introduced into Long Island Sound for spawning. This temperature rarely if ever is reached in most portions of Long Island Sound. How then can interbreeding or even spawning occur as a result of this procedure? Such a situation was described by J. Nelson ('89), who states that Southern seed oysters planted in Raritan Bay, New Jersey, or more northerly points do not spawn there. Loosanoff and Engle have shown that the minimum temperature for spawning of the Long Island Sound oyster is 16.4° C. If transplanted to Chesapeake Bay they would probably begin spawning in late April or *two months* before the local oysters would spawn. Most likely the introduced Sound oysters would be spawned out before the local ones began to spawn. J. Nelson also witnessed a situation similar to this and reported it in 1891. No interbreeding is likely if such a difference in spawning dates occurs and any conservation program based on increasing vigor by hybridization with stock from other areas is doomed to failure if the oysters in the two areas are so different physiologically.

The Oyster Drill

So far we have dealt only with spawning but the critical temperatures initiating other activities of an organism may show similar differences among specimens from different regions. This is strongly suggested by a comparison of the data on the oyster drill, *Urosalpinx cinerea,* studied in several different areas of its range from Cape Cod to Florida. In some respects these data are even more illustrative because it is somewhat easier to establish the existence in the field of the time at which certain activities of the drill are initiated than it is in the case of the oyster.

Federighi ('31) reported that drills in Hampton Roads, Va., do not move at temperatures lower than 10° C, do not drill oysters in environments cooler than 15° C, and females do not deposit their

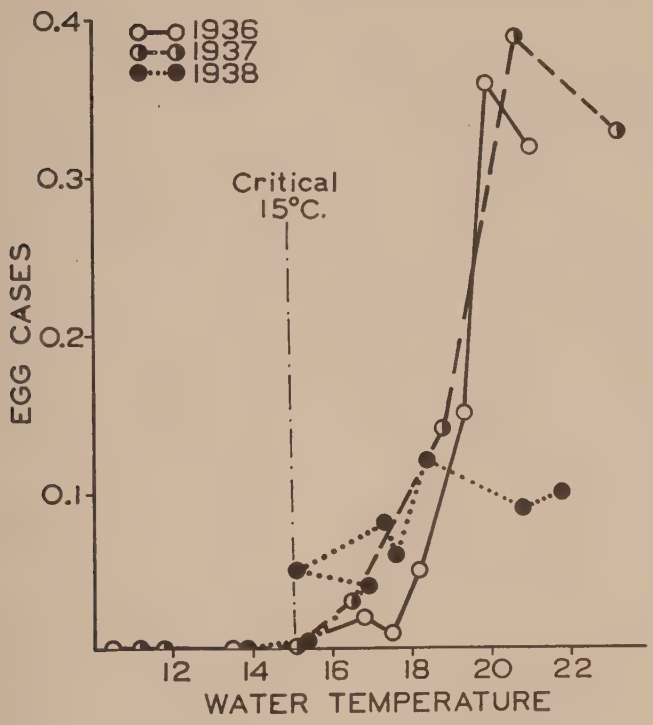

FIG. 2. Trap catches of oyster drill egg cases in 1936, 1937 and 1938 compared with the mean bottom water temperatures for all stations in the approximately weekly interval between the tending of the traps. Ordinates represent the mean number of clusters of egg cases per trap per day exposed (approximately 10 egg cases per cluster). The lines connecting the points signify the chronological order only. The line for 1937 is especially interesting since a pronounced cool spell interrupted the usual course of events.

egg cases at water temperatures below 20° C. For the years from 1936 to 1943 with the assistance of federal aid projects we conducted extensive field and laboratory studies on *U. cinerea* in the New Jersey waters of Delaware Bay. From March or April to November or December trot lines of chickenwire bag traps (J. R. Nelson, '31; Galtsoff, Prytherch and Engle, '37; and Stauber and Lehmuth, '37), baited with oysters, were raised from the oyster beds and examined for drills. This was supplemented by numerous experiments in cages in the field or in aquaria in the laboratory. During this long period an average of more than 1,500 of these traps was tended weekly. In this oyster drill control program several millions of drills were trapped altogether and even as many as 380,000 from a single 20-acre oyster ground in a season. Catches as high as 25 oyster drills per trap per day exposed were among those recorded. Almost a million egg cases were collected and the times of their appearance noted. For almost every year traps were exposed and tended for the whole annual interval when water temperatures were above 2–4° C. The data so gathered show clearly that oyster drills in Delaware Bay rarely were able to climb into the traps in water cooler than 5° C, were incapable of drilling oysters when the temperature

was below 10° C and almost without exception did not oviposit at temperatures lower than 15° C. (Some of the data for oviposition, which in the oyster drill is an individual response by mature females, is shown in figure 2.) Note that each of these critical temperature values is 5° C lower than the respective values reported by Federighi for drills in Hampton Roads, Virginia.

Moreover, Captain H. N. Gibbs, former Commissioner for Fish and Game for Rhode Island, permits me to report his unpublished findings in Narragansett Bay. In 1938 he observed egg laying on beds in 12 feet of water when the water temperature was as low as 11.1° C, a situation never seen by us in Delaware Bay.

It is interesting to note here, also, that Federighi saw the first oyster drill egg cases on May 20, 1927, at Hampton Roads, Gibbs on May 11, 1938, in Narragansett Bay and for Delaware Bay the first records for seven consecutive years range from April 26 in 1941 to May 16 in 1939. This coincidence in time of oviposition in the presence of great differences in water temperatures in the areas mentioned is especially noteworthy. Owen ('47) has already presented some evidence for chromosomal differences between size races of *Urosalpinx* in the Chesapeake area but has not yet compared drills from the several regions discussed here.

Although possibly not directly applicable in this discussion Cole ('42), reporting on *Urosalpinx* from British oyster beds, claims oviposition begins "when the sea temperature in its seasonal rise reaches 12–13° C." *Urosalpinx* was accidentally introduced into British waters from the United States, the first specimens being found in 1928 (Orton and Winkworth). In comparing his data on rate of creeping of oyster drills with those of Federighi, Cole points out that the maximum rate of creeping of the English variety occurred at 14.4° C and that at 26.5° C, the temperature used in Federighi's studies, British drills did not move at all.

Discussion

One of the most important problems to be settled experimentally is whether acclimatization is involved in the differences discussed above. Some observations have been made on the oyster, especially by oystermen but also by J. Nelson ('89, '91), but they were on transplanted stock and were not continued beyond one year. The experiments with various marine animals should be performed on as many types of physiological activities as possible contrasting under one set of conditions the behavior of specimens of the same morphological species assembled from as many geographic areas as convenient but from locations in those areas which are as nearly alike as possible with respect to other hydrographical conditions, such as salinity. Observations should be continued over a long enough span of time, at least several years, before final conclusions are drawn. Attempts at acclimatization have been made by Brown ('29) with daphnids. He finds no changes in lethal temperatures among them, even after several years culture in an experimental laboratory environment. As a result of his experiences Brown concludes that "although many animals are widely distributed, this distribution may not be due to adaptation (acclimatization) for if adaptation were general then it is even more difficult to explain the absence of forms in regions adjoining those in which they are found."

The presence of such physiological species, each the result of selection over long periods of time in situations almost completely isolated from each other and with quite different hydrographical conditions, might explain, for example, some of the other differences already reported between oysters from different areas (Loosanoff and Engle, '47). Caution is suggested in generalization on the basis of observations on a single variety under

study until the nature of these temperature variants is adequately disclosed.

Whether these groups of physiologically different organisms will ever be called true species is, however, a problem which the systematists must decide for us.

Summary

The evidence for physiological species of oysters and oyster drills has been presented. The probability has been raised that other marine inshore invertebrates may also be shown to contain physiological varieties within the designation of the usually accepted morphological species. Finally, the practical importance of such information has been cited to demonstrate the need for additional observations and to stimulate the interest of others in this problem.

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AN ECOLOGICAL SURVEY OF THE SUBTROPICAL INSHORE WATERS ADJACENT TO MIAMI[1]

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A considerable amount of investigation has been carried out into the general ecology of the shallow water life of temperate seas, particularly with regard to the sedentary organisms, the literature of which is summarized by McDougal ('43), Scheer ('45) and Smith ('46). The food cycles, breeding seasons, succession and growth under various conditions have principally been studied. A relatively small amount of attention has been devoted to the quantitative relationships existing between the dissolved inorganic and organic nutrients, the plankton and the animal and plant communities, and much of this has been restricted to special interests such as the shell fish industry. Considerably more fundamental study has been given to such relationships and to the associated problems of organic production in fresh water and even in the less accessible open ocean. It is also true that, compared to temperate regions, the tropical waters have been greatly neglected in these respects. The outstanding exception to this generalization is the careful and painstaking work of the Great Barrier Reef Expedition, which dealt, however, with a somewhat specialized situation.

The general paucity of quantitative information regarding the chemical, physical and biological conditions in the Miami area, in addition to the considerations mentioned above, prompted the investigations which form the subject of the present report. They were designed rather to outline the range of general conditions and their interrelations in subtropical shallow waters than to provide detailed information on any specific circumscribed problem.

In carrying out the work a considerable amount of data was accumulated. It would be impracticable to present this except in summarized form. It is hoped, however, that more detailed presentations may be offered elsewhere as investigations are carried out into more specific problems arising out of the present survey.

The observations were made at a series of stations covering a wide range of environmental conditions. Chemical and physical observations and plankton samples were made at intervals of approximately one month during 1945 and 1946. A wooden float, containing racks for glass collecting panels, was anchored at each station for the purpose of recording breeding seasons, attachment density, growth rate and succession of sessile organisms.

In the sometimes difficult task of making observations and of replacing floats lost during storms the authors were assisted at various times by Albert Schwartz, C. E. Dawson and J. Q. Tierney. Chemical determinations were made by Robert H. Williams, and plankton examination was carried out by Charles C. Davis. Credit should also be given to Mrs. Dorothy Clum Morse who originally began the plankton studies. Examination of the glass collecting panels was carried out by F. G. Walton Smith.

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Location of the Stations

Ten of the stations were located in Biscayne Bay, which is at the southeast

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end of the Florida peninsula between 25° 23′ and 25° 55′ North latitude and between 80° 08′ and 80° 21′ West longitude. It is elliptical in shape, 32 nautical miles long and up to 8.6 nautical miles wide. As shown in the map (fig. 1) it is bordered on the west by the mainland from Miami southward. The northern part of the bay is bounded to the eastward by a chain of keys starting with Miami Beach. The central part of the bay is separated from the Atlantic Ocean by broad coral banks covered with sand, shell and mud which continue south of the line of keys and which are only partly exposed at low tide. They are known as the Safety Valve. The small island of Soldier Key is the only land raised above these sand flats at high tide. The southern part of the bay is separated from the ocean by Elliot Key and from the rest of the bay by an east-west shoal, Featherbed Bank.

The bay is very shallow, mostly from eight to eleven feet deep; the maximum depth is fifteen feet; much of the northern and western portion of the bay is less than six feet deep.

The tide flows rapidly in and out of the bay between the keys and through several deeper channels in the central flats. The flooding tide flows southward over Featherbed Bank. Currents elsewhere in the bay have not been charted. Between the line of keys and flats on the one hand and the outer coral reefs such as Fowey Rocks and Triumph Reef on the other is a southward flowing counter current in the lagoon channel. The northward flowing Florida Current or Gulf Stream is farther east beyond the outer coral reefs.

The eleven stations where the samples were collected over a period of a year, as shown on the map (fig. 1), were chosen to represent ecologically distinct habitats. The Beach Boat Slips station (No. 1) was considered representative of the northern bay where moderate amounts of sewage were present. The N. E. 18th Street, Miami, station (No. 2) was located within 100 feet of the end of a large city sewer from which raw sewage entered the bay. These stations were the only ones immediately adjacent to the built-up dock and city areas. Sea walls, offering good attachment for sedentary organisms, extend for several miles north and south of these places and are absent at the locations which were selected for the remaining stations. On both east and west sides of the northern bay the tidal currents run strongly north and south.

The station north of Hurricane Harbor on Biscayne Key (No. 3) was chosen to compare with the station in Hurricane Harbor (No. 4), a dredged harbor fifteen to twenty-five feet deep, almost completely land locked, but without any sewage inflow.

The Biscayne Channel (No. 5) and Soldier Key (No. 10) stations are similar in that both are located in deep channels between bay and ocean, through which strong tidal currents run. The former differs by proximity to the land mass of Biscayne Key. The Chicken Key station (No. 11) is close to the mainland and to the mouth of artificial drainage channels, but without the sewage which enters the northern part of the bay. It is more exposed to wind and wave action than most of the other stations in the bay. Featherbed Bank (No. 6) was chosen as in intermediate situation between the isolated water to the west of Elliot Key (No. 7) and the rapidly circulating tidal waters at Soldier Key (No. 10). It lies at the entrance to a dredged channel through Featherbed Bank, connecting the central and southern parts of the Bay.

East Elliot Key (No. 8) was chosen to represent the shoreline of the ocean bathed by the southward drift. The shore here is sandy with low rocky exposures and very little mangrove. The western shore of Elliot Key (No. 7) is partly fringed with mangroves. Both of these stations are in about three feet of water at low tide, over a sandy bottom.

Triumph Reef (No. 9) on the line of

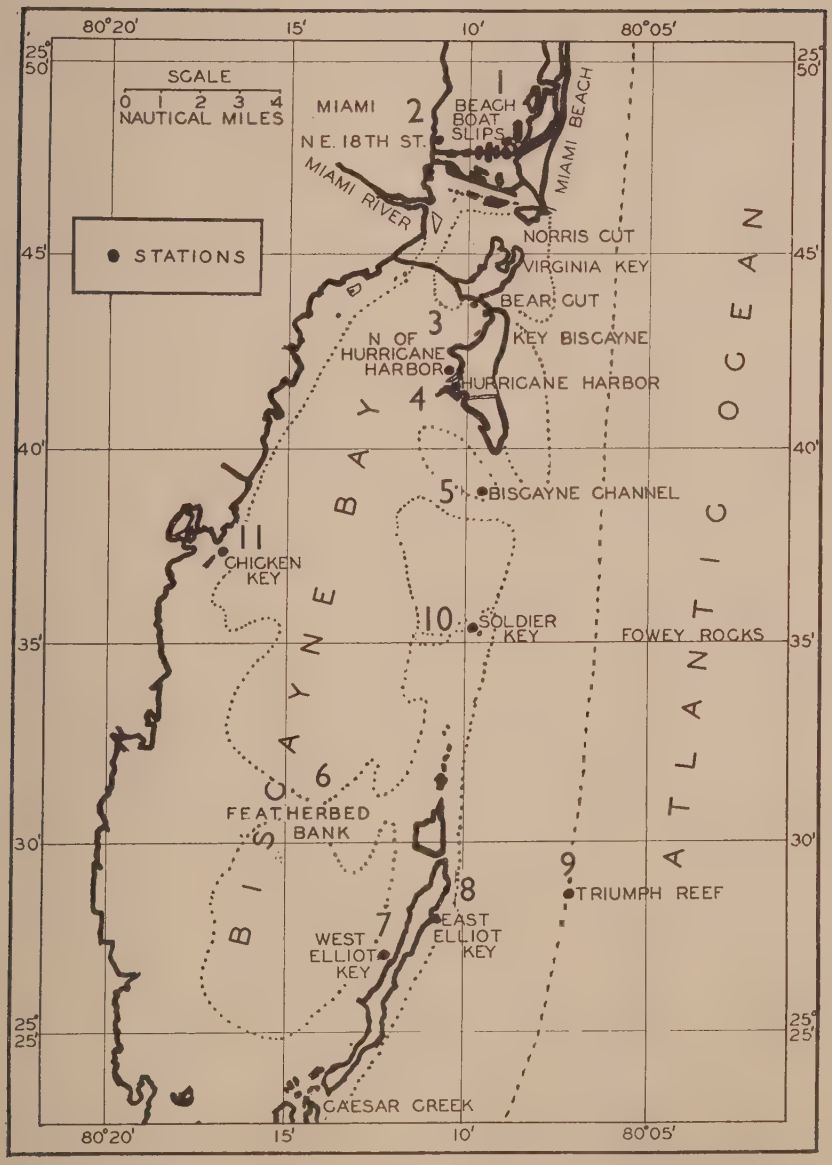

FIG. 1. Map of Biscayne Bay and vicinity. Numbers refer to stations. . . . . 1 fathom and 50 fathom contours.

reefs near the margin of the Florida Current is in about twenty feet of water. The prevailing onshore winds from the southeast bring a drift of surface ocean water across the reef.

PHYSICAL AND CHEMICAL CONDITIONS

Chemical and physical observations were chosen which would be most useful in correlating with the distribution of the plankton and attached organisms,

and which could be determined accurately with the limited equipment and facilities available. These were: temperature, a factor influencing all biological activity; salinity; dissolved oxygen, an indicator of the photosynthesis-respiration balance; phosphate-phosphorus, an essential mineral which is often a limiting factor for plant growth in the sea; and nitrite-nitrogen, intermediate between ammonia and nitrate in the nitrogen cycle in the sea.

Analytical methods used were those described in mimeographed "Methods of Oceanographic Chemistry," prepared by Rex J. Robinson and Thomas G. Thompson, Oceanographic Laboratories, University of Washington. Salinities were calculated from the results of silver nitrate titrations. Dissolved oxygen was determined by the standard Winkler method. The methods for phosphate and nitrite have since been published (Robinson and Thompson, '48a, '48b).

Data obtained from the analyses of surface samples at the eleven stations between July 1945 and June 1946 are summarized in tables I to VI. The seasonal variations in sea temperature (table I) show the expected correlation with air temperatures and total hours of sunshine, as reported by the U. S. Weather Bureau. The sea temperature reached its lowest point at all stations in December and then increased rapidly in the spring. All stations except Triumph Reef showed similar seasonal variation in temperature, varying from the extremes of 18.25° C

TABLE I. *Sea water temperatures at the surface*

Degrees Centigrade

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	30.2	31.2	31.3	32.0	31.3	32.0	32.0	32.3	29.4	31.7	—
8–4–45	29.7	29.8	29.7	30.7	30.1	30.5	30.5	30.5	29.8	30.5	30.5
10–27–45	24.62	24.88	24.93	25.30	25.00	26.87	27.90	27.68	26.68	24.70	26.80
12–2–45	20.55	21.93	20.20	19.93	21.50	18.25	19.06	19.15	24.35	19.58	18.35
1–6–46	21.80	22.00	21.18	21.10	21.70	21.30	21.30	—	—	21.79	22.47
2–3–46	22.70	22.70	21.93	22.70	22.45	23.15	22.85	22.78	25.00	23.23	24.08
4–28–46	26.12	27.00	24.68	25.28	25.60	24.67	24.91	24.12	25.35	25.15	28.57
6–6–46	28.58	27.82	28.28	29.35	28.00	29.12	28.90	29.05	27.60	28.13	29.78

TABLE II. *Sea water salinities at the surface*

Grams per kilogram

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	37.35	37.52	38.04	38.69	37.35	39.09	38.97	37.40	36.36	37.11	—
8–4–45	36.38	36.24	37.71	37.83	36.97	38.08	39.26	36.82	35.62	36.67	35.47
10–27–45	29.67	27.36	30.95	30.99	32.41	35.61	35.19	35.52	35.25	33.06	29.85
12–2–45	32.41	27.01	31.69	31.11	34.41	33.71	34.09	34.43	36.04	33.91	29.34
1–6–46	29.33	24.92	34.67	33.13	35.14	35.41	35.37	—	—	36.22	28.97
2–3–46	34.25	28.66	34.63	34.47	35.59	36.58	36.56	36.65	36.02	36.26	33.19
4–28–46	36.80	35.63	38.24	38.26	36.96	38.32	38.06	37.25	36.50	36.86	38.22
6–6–46	34.29	30.17	35.10	35.23	35.50	37.39	36.36	36.22	36.08	35.70	32.14

TABLE III. *Dissolved oxygen in sea water at the surface*
Milligram atoms per liter

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	.349	.355	.380	.351	.394	.441	.297	.377	.375	.408	—
8–4–45	.313	.386	.350	.288	.380	.445	.342	.405	.430	.451	.403
10–27–45	.342	.312	.351	.397	.426	.394	.401	.488	.416	.453	.347
12–2–45	.428	.401	.467	.421	.453	.465	.493	.525	.434	.436	.428
1–6–46	.383	.386	.438	.354	.258	.443	.438	—	—	.416	.410
2–3–46	.384	.287	.432	.356	.363	.456	.448	.480	.424	.492	.445
4–28–46	.416	.381	.448	.456	.458	.492	.446	.491	.447	.478	.517
6–6–46	.307	.178	.369	.336	.394	.431	.374	.393	.408	.400	.452

TABLE IV. *Dissolved oxygen in sea water at the surface*
Per cent of saturation

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	88.5	91.7	98.6	92.3	101.6	116.5	78.3	98.6	93.3	105.8	—
8–4–45	78.3	96.6	88.6	74.2	96.0	111.6	88.7	103.0	106.7	114.7	101.5
10–27–45	74.7	67.5	77.7	88.5	95.3	93.2	96.3	117.0	97.5	101.1	78.6
12–2–45	89.0	82.2	96.0	85.7	96.9	93.6	101.0	107.9	98.5	89.9	84.0
1–6–46	79.6	78.4	93.1	74.5	55.6	95.1	93.9	—	—	90.5	86.1
2–3–46	83.4	60.2	92.9	77.5	79.6	101.8	100.0	106.6	97.5	109.8	98.5
4–28–46	98.3	90.3	104.6	107.9	105.0	115.2	104.6	112.4	103.4	112.1	128.8
6–6–46	74.2	41.2	89.2	82.9	95.0	107.6	92.1	97.1	98.3	96.7	109.7

in winter to 32.2° C in summer, with a range of 14° C.

This is a greater seasonal variation than that found by Orr ('33a) in the Great Barrier Reef lagoon in Australia, where the extreme range was 8.6° C. This difference is partly to be explained by the fact that the lagoon was considerably deeper (to 40 meters) than Biscayne Bay. Dole ('14) reported temperature determinations at some of these Florida stations on June 23, 1913, which averaged 1.4° C cooler than those on June 6, 1946. This difference is probably the result of weather variations.

Triumph Reef water was cooler in summer and warmer in winter than water at any other station; it varies from 24.35° to 29.8° C. This small range is characteristic of oceanic conditions and is probably due to the water at Triumph Reef mixing with water from deeper parts of the Florida Current.

Salinities (table II) at all stations except Triumph Reef show the expected correlation with rainfall. Lowest salinities were found at the station at N. E. 18th Street, Miami, where fresh water from sewer and drainage outlets further diluted the sea water. The ocean at Triumph Reef showed the least changes in salinity, probably because vertical and horizontal exchange with ocean water nearby distributed the rain water quickly.

Dole ('14) reported chlorinity determinations on water at some of these stations June 23, 1913, which were less than 0.7‰ above or below those on June 6,

TABLE V. *Phosphate-phosphorus in sea water at the surface*
Microgram atoms per liter

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	<0.03	<0.03	<0.03	<0.03	<0.03	<0.03	<0.03	<0.03	<0.03	<0.03	—
8–4–45	<.03	.03	<.03	<.03	.00	.00	.00	.00	.00	.00	.00
10–27–45	<.03	.12	.00	.00	.00	.00	<.03	<.03	.00	<.03	.00
12–2–45	.00	1.20	.00	.00	.03	.00	.00	<.03	.10	.00	.00
1–6–46	.00	.00	.00	<.03	<.03	.00	.00	—	—	.00	.00
2–3–46	.00	1.5	.00	.00	.00	<.03	<.03	.00	.00	.00	<.03
4–28–46	.03	.72	.00	.00	<.03	.03	.06	<.03	.00	.00	.00
6–6–46	.06	2.4	.03	.03	<.03	.00	<.03	<.03	.00	<.03	<.03

1946. The water in the lagoon behind the Great Barrier Reef of Australia (Orr, '33a) had an average salinity of about 33.4‰ and annual range of 4.2‰. Average of the mean of seasonal ranges of all stations in south Florida is 34.7‰ and the average annual range is 6.2‰.

The dissolved oxygen content (tables III and IV) was near saturation at all stations away from pollution. The lowest oxygen content was found after five and one-half hours of ebbing tide at the N. E. 18th Street station on June 6, 1946. The sewage here would contain much unsaturated material which reacts with the iodine liberated by Winkler's method and thus the results probably indicated a lower oxygen content that actually exists in the water. However, the abundant bacteria in such water probably reduce the oxygen considerably.

McClendon ('18) reported that the sea water in the shallow areas of the Dry Tortugas, Florida, was generally slightly supersaturated with oxygen during the day and undersaturated at night. Orr ('33a) reported that the sea water in the lagoon behind the Great Barrier Reef was usually 90 to 100% saturated, only once supersaturated, and only for a short period below 90% saturated. A wider range of oxygen concentration, 55 to 120% of saturation, was reported by Orr ('33b) for another station inside the Great Barrier Reef. Riley ('39) reported 99% saturation in a sample of water taken at one meter depth at his station 3492, fifteen nautical miles south of Triumph Reef. At this station, on May 16, 1939, he found that water contained more oxygen at a depth of 48 meters than at the surface. In the latitude of 15° South in the Atlantic Ocean, Wattenberg ('29) reported that the high oxygen content at the surface extends downward to about fifty meters, then decreases rapidly.

For purposes of correlation with plankton and fouling organism distribution, the phosphate and nitrate data are probably the most significant. The method used for phosphate determination measures as little as 0.03 microgram atom per liter. Samples which showed distinguishable color but less than the most dilute standard were recorded as "less than (<) 0.03 μg. atom/L." If no color formed at all, they were recorded as "0.00."

The only significant phosphate (table V) was found at the 18th Street station near the outlet of the city sewer. This phosphate is probably derived from bacterial decomposition of phosphoproteins and other organic phosphorus compounds in the sewage.

The apparent almost complete absence of phosphate at most of the stations may be the result of phytoplankton growth using up phosphate in the surface layers and failure of replenishment from phos-

phate-rich deeper waters of the ocean, where Riley ('39) found up to 1.82 milligram atoms of phosphate per cubic meter of water at a depth of 184 meters at his station 3942 which is outside the reef and fifteen miles south of Triumph Reef. His sample at that station from a depth of one meter on May 16, 1939, contained 0.06 mg. atom per cubic meter (equals 0.06 microgram atom per liter). Our samples taken down to 15 meters outside Triumph Reef usually contained no measurable phosphate.

The phosphate content of south Florida inshore waters is much lower than that in the lagoon behind the Great Barrier Reef, reported by Orr ('33a), which averaged about 5 mg. phosphate-phorphorus per cubic meter (0.16 μg. atom per liter). Seasonal changes in phosphate and dissolved oxygen are negligible in both areas. Low phosphate values are characteristic of surface waters of tropical seas in general (Atkins, '26; Hentschel and Wattenberg, '30; Rakestraw and Smith, '37).

Nitrite is more abundant than phosphate. Measurable quantities of nitrite (table VI) were found at most stations (except Triumph Reef) throughout the year except in December, which is the month of the lowest temperatures. The seasonal maximum at most stations occurred in February. The high nitrite values (to 2.0 microgram atoms per liter) were found at the Miami and Beach Boat Slips stations. This nitrite is probably the product of bacterial oxidation of ammonia from nitrogenous compounds pouring out of the sewers nearby. Further oxidation would be expected to produce nitrate which would stimulate phytoplankton growth. The organic material in the sewage would be expected to stimulate growth of certain marine animals which can use it for food.

The absence or near-absence of nitrite in the ocean water at Triumph Reef most of the year suggests that in the ocean most of the nitrogen has been oxidized to nitrate and used by the phytoplankton. In the shallow water of the bay, decay of organic matter on the bottom probably renews the nitrite content. It is possible that the sharp decrease in temperature in December slowed these bacterial oxidations in the unpolluted water, so that the phytoplankton might entirely remove the diminished supply of inorganic nitrogen.

Such variations in nitrite are to be expected under the variable conditions of these stations (Rakestraw, '36).

Plankton

Methods

All samples were obtained from near the surface by means of a Clarke-Bumpus net of No. 20 mesh. In each case the net was towed for a standard period of ten minutes at a constant engine speed in order that the volumes of the samples

Table VI. *Nitrite-nitrogen in sea water at the surface*
Microgram atoms per liter

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	0.1	0.3	0.1	0.15	0.1	0.1	0.1	<0.1	0.0	0.1	—
8–4–45	.2	.25	.1	.1	.05	.1	.1	.0	.0	.0	.1
10–27–45	.8	1.6	.3	.25	.3	.15	<.1	.0	.0	.15	.2
12–2–45	.15	.8	.15	.1	.0	.0	.0	.0	.0	.0	.0
1–6–46	.8	1.0	.2	.1	.1	.1	.2	—	—	.2	.1
2–3–46	.4	2.0	.4	.4	.4	.1	.2	1.6	.2	.2	.4
4–28–46	.2	.2	.15	.2	<.1	<.1	.1	<.1	<.1	.1	<.1
6–6–46	.6	1.0	.15	.2	.2	.15	.15	.1	<.1	.1	.25

TABLE VII. *Plankton volumes in milliliters*

Date	Stations										
	1 Beach Boat Slips	2 N. E. 18th Street, Miami	3 N. of Hurricane Harbor	4 In Hurricane Harbor	5 Biscayne Channel	6 Featherbed Bank	7 West Elliot Key	8 East Elliot Key	9 Triumph Reef	10 Soldier Key	11 Chicken Key
7–7–45	12.8	22.9	11.0	21.1	6.4	2.8	<1.0	<1.0	<0.5	0.5	—
8–4–45	2.0	3.0	0.5	0.5	<0.5	0.5	2.0	0.5	1.0	1.0	<0.5
10–27–45	1.0	<1.0	3.5	5.5	0.5	trash	3.0	4.0	4.5	5.0	5.0
12–2–45	<0.5	2.5	15.0	7.5	2.0	2.5	<0.5	2.5	2.5	2.5	5.5
1–6–46	13.0	5.0	2.0	2.0	1.0	—	—	—	—	—	—
2–3–46	1.0	2.0	5.0	4.0	2.0	0.75	0.5	0.5	0.5	0.5	1.5
4–28–46	0.75	1.0	1.0	1.0	0.5	0.5	1.5	0.5	1.0	0.5	1.0
6–6–46	10.0	4.5	1.0	0.5	0.5	0.75	0.25	0.5	0.25	1.0	1.0

might be comparable. Defective action of the counter on the net prevented the determination of the exact volume of water passed at each station.

In the laboratory, a small portion of the thoroughly mixed sample was examined microscopically. The first 200 organisms encountered were listed in order to obtain an idea of the composition of the plankton, its dominant species and their relative abundance. In the case of chain-forming diatoms, each chain encountered was considered to be a single organism. This method has the obvious disadvantage of neglecting size differences between the several organisms.

The volume of each sample was obtained after microscopical analysis by a water displacement method. The volume of the plankton plus the suspending water was obtained after which the sample was filtered through standard smooth-surface chemical filter paper, which had previously been wet with tap water. A measurement of the volume of the filtrate then made possible the calculation of the plankton volume.

Volume

The volumes of samples obtained in Biscayne Bay and vicinity by the above method varied from 0.25 ml. at several localities to a maximum of 22.5 ml. at Station 2 in July, 1945 (table VII). In general, the largest volumes were found at Stations 1, 2, 3, and 4, the first two in polluted regions, the other two in unpolluted, but protected locations in the northern portion of the bay. Lowest average volumes were found at Stations 6 and 7, in the southern part of the bay. Maximal volumes were always associated with a high percentage of diatoms.

Stations in the northern portion of the bay (Nos. 1, 2, 3, 4 and 5) show two maxima, one in July 1945, and a smaller maximum in December–January. The remaining stations, all located in the southern portion of Biscayne Bay, or in the ocean outside Elliot Key, which delimits the southern portion, show only one maximum, in October 1945. One exception to this statement is Featherbed Bank (No. 6), which shows a small maximum in July 1945, and a second in December, as in the northern stations. However, the July maximum is very small, and volume was not measured for the October sample because of the presence of considerable trash consisting largely of broken turtle grass and other detritus. In addition to the above, Stations 1 and 2 show a third maximum in June 1946, apparently corresponding to the maximum of the previous July. This does not appear markedly at any of the other stations.

Diatoms

Diatoms were important in nearly every sample in the present study, at times constituting as much as 99.5 per cent of

the total organisms. However, in the southern part of the bay (Nos. 6, 7), they were relatively unimportant.

In the northern portion of the bay and in Biscayne Channel, the diatoms were always the most important ingredient of the plankton, with the exception of outside Hurricane Harbor (No. 3) during April and June, when they were exceeded by the dinoflagellates. These stations were characterized by the dominance especially of species of *Chaetoceros, Rhizosolenia,* and to a lesser degree, *Bacteriastrum. Thalassiothrix nitschioides* was relatively abundant in all but one of these northern stations in December, but not at any other time of the year.

In the remaining stations, located in the southern portion of the Bay, or outside of Elliot Key, which bounds the southern portion, the abundance of the diatoms was more variable. At Soldier Key (No. 10) they were always the most important ingredient, but at all the other stations they were a minor, though still important portion of the plankton in one or more of the observations. Featherbed Bank (No. 6) and west of Elliot Key (No. 7), especially, were characterized by having a plankton population poor in diatoms for the whole year. At West Elliot Key the diatoms at no time constituted the major portion of the plankton.

The diatom population of the southern stations, with the partial exception of Soldier Key (No. 10), was very different from that of the northern stations (Table VIII). In the place of *Chaetoceros, Rhizosolenia* and *Bacteriatrum,* the predominant diatoms, when any individual group of diatoms was dominant in the plankton, were the naviculoids, *Striatella unipunctata* and occasionally other forms. In October, December and June, Soldier Key had characteristics similar to the northern stations. At other times it was similar to the southern stations. Also, in December, all but West Elliot Key of the southern stations and all the northern stations had species of *Chaetoceros* as dominant forms.

TABLE VIII. *Genera of dominant diatoms*

Station	July	Aug.	Oct.	Dec.	Jan.	Feb.	Apr.	June
1	Chaetoceros	Rhizosolenia	Chaetoceros–Skeletonema	Chaetoceros Thalassiothrix	Chaetoceros	Chaetoceros Nitzschia Rhizosolenia	Chaetoceros Nitzschia	Chaetoceros Nitzschia Rhizosolenia
2	Chaetoceros Rhizosolenia	Rhizosolenia	Chaetoceros	Chaetoceros Thalassiothrix	Chaetoceros	Chaetoceros Rhizosolenia	Chaetoceros	Rhizosolenia
3	Chaetoceros	Chaetoceros	Bacteriastrum Chaetoceros	Chaetoceros	Chaetoceros	Chaetoceros	Naviculoids	Chaetoceros
4	Chaetoceros	Chaetoceros	Bacteriastrum Chaetoceros	Chaetoceros Thalassiothrix	Chaetoceros	Bacteriastrum Chaetoceros	Chaetoceros	Bacteriastrum Chaetoceros
5	Chaetoceros	Chaetoceros	Bacteriastrum Chaetoceros	Asterionella Chaetoceros Thalassiothrix	Nitzschia	Chaetoceros Naviculoids	Naviculoids	Chaetoceros
6	?	?	Bacillaris	Chaetoceros	—	None	Naviculoids	None
7	?	?	None	None	—	None	Naviculoids	None
8	?	?	None	Chaetoceros Melosira	—	None	Naviculoids	None
9	?	?	None	Chaetoceros	—	? Licmophora	Naviculoids	Asterionella
10	?	?	Chaetoceros Nitschia	Chaetoceros	—	Naviculoids Striatella	Naviculoids	Naviculoids Rhizosolenia
11	—	Strictella Rhabdonema	None	Chaetoceros	—	Naviculoids	Naviculoids	Naviculoids

Dinoflagellates

The dinoflagellates were usually subordinate to the diatoms in abundance in the plankton of Biscayne Bay and vicinity, but there were some important exceptions, mostly in the southern part of the region. Outside Hurricane Harbor (No. 3) in the northern portion of the bay, however, the dinoflagellates constituted the major ingredient of the plankton on the April and June 1946 cruises, amounting to 31 per cent and 60.5 per cent of the total organisms respectively. This was due in the former case to the abundance of *Ceratium furca,* and in the latter case to a flowering of a species of *Gonyaulax.*

Among the southern stations, the dinoflagellates were especially important at Featherbed Bank (No. 6) and West Elliot Key (No. 7), a region that seems somewhat exceptional in many respects. At Featherbed Bank (No. 6) the dinoflagellates were important ingredients of the plankton in every sample and in February and June respectively they constituted 80.5 per cent and 52.0 per cent of the total plankton. At West Elliot Key (No. 7), and the other southern stations, the dinoflagellates were usually of considerable importance, especially during February.

Of the various dinoflagellata occurring in the region, it was found that *Ceratium furca* and species of *Gonyaulax* are the most likely to be dominant, and of these *C. furca,* even when not dominant, is almost universally present.

Animals

The use of a fine meshed net alone did not lead to an accurate picture of the total animal population, particularly the larger forms, such as copepods. Nevertheless, some of the results are of interest, both in regard to the smaller forms and to the larger forms.

The samples collected during April show, in general, the largest percentages of animals. This was a month of uniformly low plankton volumes at all the stations (table VII). Further studies will be necessary to ascertain whether these results indicate a greater *number* of animals per unit volume of seawater, or simply that the animal population is more conspicuous because of the absence of a masking bloom of plant life. From the present samples it is possible to estimate roughly that the animals are actually present in smaller numbers per unit volume of seawater, as would be expected when their natural food is sparse.

Considering the copepods, copepod nauplii and tintinnids alone as the most important and regular members of the plankton population it can be seen that during the year studied none of these forms was ever dominant at stations in the upper bay (Nos. 1, 2, 4) and that, at the other extreme, one or more of these forms were dominant in every observation except that for July 1945 at Stations 7 and 8, located in the southern part of the territory (Nos. 7, 8) (table IX). Stations 6, 9 and 11 also had one or more of these forms dominant on three of the visits, while Stations 3, 5 and 10 had one or more of the forms dominant only on one inspection. Thus, as was the case with the diatoms and the dinoflagellates, there is again a differentiation between northern and southern stations. This is not a differentiation between inside and outside stations, such as the preliminary results indicated might be the fact, since at Triumph Reef (No. 9), near the edge of the Gulf Stream, the copepoda, copepod nauplii or tintinnids were dominant on only three of the visits (October, April and June), whereas West Elliot Key (No. 7) in the bay had one or more of of these forms dominant at all times except July 1945.

The highest percentage of tintinnids occurred west of Elliot Key in June 1946 (38.5 per cent) but Triumph Reef ran a close second with 37.5 per cent in April. On the other hand, to the east of Elliot Key (No. 8), in the ocean, but protected by the outside reefs, tintinnids

TABLE IX. *Copepoda, copepod nauplii and tintinnids, by station number and date*

Station	1	2	3	4	5	6	7	8	9	10	11
July, 1945											
Copepoda	—	p	p	—	p	—	—	—	p	p	?
Copepod nauplius	p	p	p	p	?	p	—	—	—	p	?
Tintinnids	p	p	p	p	p	—	—	p	—	p	?
August, 1945											
Copepoda	p	—	—	—	—	p	—	—	p	p	p
Copepod nauplius	p	p	p	p	p	p	*dom*	p	p	—	p
Tintinnids	—	p	p	p	p	p	p	*dom*	p	p	p
October, 1945											
Copepoda	.5	p	—	—	p	*12*	8	5	*17*	4.5	*48.5*
Copepod nauplius	—	p	.5	p	—	*10*	21.5	19.5	6.5	7	4.5
Tintinnids	.5	—	p	.5	p	.5	6.5	4	.5	.5	2
December, 1945											
Copepoda	1	—	—	—	—	—	—	—	—	—	—
Copepod nauplius	3	p	—	.5	—	8.5	*19.5*	*13*	1.5	1	.5
Tintinnids	.5	—	—	—	—	—	3	.5	—	—	—
January, 1946											
Copepoda	—	.5	—	.5	—						
Copepod nauplius	p	3	2	p	2						
Tintinnids	—	—	1.5	—	3.5						
February, 1946											
Copepoda	.5	p	p	p	—	1	1.2	2.5	2.5	2.5	4.5
Copepod nauplius	p	.5	.5	p	.5	4	*11.3*	*12*	5	5	5.5
Tintinnids	p	p	p	—	1	3.5	.6	*14*	4.5	7.6	2.5
April, 1946											
Copepoda	2.4	1	*10.5*	3.5	5	6	*11.8*	4	1.5	2	1
Copepod nauplius	8.3	2.5	*15*	2.5	*13.5*	*21.5*	*19*	7.5	6	20	*17.5*
Tintinnids	2.6	.5	1.5	3.5	*15.5*	7	*12.2*	*17*	*37.5*	4	2.5
June, 1946											
Copepoda	p	—	1.5	2.5	2	2.5	1.5	5	*11.5*	p	*16.5*
Copepod nauplius	p	p	6	1.5	8	*13.5*	*13.5*	*11*	*12*	1.5	6.5
Tintinnids	p	.5	4.5	p	9	*20.5*	*38.5*	*32.5*	3	1.5	9

(p) The organism was observed and present in the sample.
(—) The organism was not observed.
(*dom*) The organism was dominant, though the percentage was not determined.
Numbers indicate percentage of total organisms.

were a dominant form on four observations. This was less often the case at any of the inside stations, or at Triumph Reef, which is located farther out in the ocean.

Copopod nauplii were more widely distributed than the tintinnids, though even the latter were seldom completely absent from any of the samples. Copepod nauplii were usually one of the dominant forms at Stations 7 and 8, but were also dominant and even more abundant at times in some of the other stations, mostly in the southern portion of the area studied.

The copepoda (both immature copepodid stages and adults) were seldom a very considerable percentage of the total organisms, but their relatively large size made them more important than the percentages would indicate. Most of the copepoda found, however, were of relatively small species. The highest percentages were obtained twice at the same station at widely different dates, namely at Chicken Key (No. 11), near the main-

land in the southern portion of the bay. In October 1945, 48.5 per cent of the total organisms were copepoda, and in June 1946, 16.5 per cent of the total organisms were copepoda. In the latter instance, over one-third were adult copepods, belonging to all three sub-orders, the Calanoida, Cyclopoida and Harpacticoida. Copepoda were also a very large percentage of the plankton on two separate occasions at West Elliot Key.

General composition of the samples

It is frequently stated that the plankton of tropical waters, as distinguished from that of temperate and frigid waters, is sparse, but contains many species. The present investigation tends to bear out the sparseness of the plankton population at most times of the year. However, at times of diatoms maximum in Stations 1, 2, 3 and 4 in the northern portion of the bay, the volume of the plankton was considerable, considering the small type of net used.

On the other hand, there was little to distinguish the samples from those from temperate seas as far as number of species involved was concerned. In temperate seas plankton samples usually contain as many species (though frequently different forms are involved, of course) as were found in the Biscayne Bay area. Conversely, some of the Biscayne Bay samples were sparse in the number of species involved. In the upper bay (Nos. 1, 3, 4, 5) in July 1945, 95 to 99 per cent of the total organisms were species of *Chaetoceros*. In August a species of *Rhizosolenia* constituted 95 to 99 per cent of the total organisms at Station 1, and over 90 per cent at Station 2. In January, two species of *Chaetoceros* constituted 91 per cent of the total organisms. Finally, in June 1946 a species of *Rhizosolenia* constituted 90 per cent of the total organisms at Station 2. It is true that all these stations are in the northern portion of the area studied and that this may be an unusual situation for tropical waters, but comparable samples obtained in connection with Bird Island studies in the Gulf of Mexico showed 86.5 per cent *Ceratium furca* at the station located at Green Key, Tampa Bay and 85.5 per cent *Skeletonema costatum* at the station located in the N. W. Terra Ceia Bay.

Data on fouling organisms

Very little direct evidence was obtained on the prevalence of fouling organisms (table X). The larvae of barnacles of bryozoa and of the tunicates very seldom occurred in any numbers, nor did they tend to occur more frequently in those areas where fouling was more intense.

TABLE X. *Distribution of larvae of certain fouling organisms*

(Numbers indicate station numbers)

Month	Barnacle nauplii	Barnacle cyprids	Bryozoa	Tunicates
July	none	none	none	9?
August	1	1, 2, 6, 7, 9	none	4?, 5?
October	6, 7, 8	4, 5, 7, 8, 10	none	10?, 11?
December	none	none	none	none
January	2, 3	5	none	none
February	none	7, 11	4, 10	none
April	1, 2, 11	10, 11	none	4
June	none	11	none	11

Two probable reasons for the rare occurrence of the larval forms of fouling organisms are (1) A probably very short pelagic life for the organisms and (2) The tendency of these forms to swarm in large numbers, so that they are picked up by the net only by accident if it happens to pass through a swarm. In the future, more adequate means of studying the occurrence of the larval forms of fouling organisms in their pelagic environment should be devised.

Effect of pollution

Station 1, and especially Station 2, were located in a highly polluted area, close to the cities of Miami Beach and Miami, respectively. It was expected that the sewage pollution at these stations would have a marked effect on the plankton by enriching the water with nitrates and phosphates. Chemical conditions

show that the phosphate content of the water is decidedly higher at Station 2 than elsewhere in the area and that nitrite nitrogen is higher at both Stations 1 and 2.

The highest plankton volume of any obtained in this investigation was found at Station 2 in July 1945, but the average plankton volume over the year at Stations 1 and 2 was only very slightly higher than that at Stations 3 and 4, which are located at some distance from polluted areas and which show typically low amounts of nitrite and phosphate. Stations 1, 2, 3, and 4 have much higher volumes than those obtained in any of the other stations. All these stations are in the upper bay.

With the data at hand, it is difficult to state the reason for the high plankton volumes at Stations 3 and 4, outside of the polluted area. It is necessary to keep in mind that the bay water is not static, but is constantly moving. Increased plankton growth, stimulated by the influx of phosphorus-rich and nitrogen-rich sewage from the metropolitan area, might be carried by the currents down the bay. Subsequently, as the initial growth of plankton died, decay would liberate nutrient salts, which would immediately be used by other phytoplankton organisms. On the other hand, the evidence from this investigation shows that the winter plankton maximum in the two unpolluted stations occurred a month earlier (December) than it did in the two highly polluted stations (January). Also, the average plankton volume outside Hurricane Harbor (No. 3) in the open Bay, and hence subject to the influence of up-bay water, was somewhat lower than that inside the nearly land-locked harbor, which is thus cut off from outside influences to a greater extent. The mangrove swamps in this vicinity may possibly have contributed nutrient materials.

During most of the year these stations had essentially the same dominant species of diatoms as the northern stations (Nos. 1, 2) but during April outside Hurricane Harbor was similar to the southern stations. Inside the harbor, however, the plankton was still characterized by *Bacteriastrum* and *Chaetoceros* as dominants. This seems to indicate a northward movement of southern water in April, cutting off Hurricane Harbor.

Effect of low nitrite and low phosphate

Nitrites and phosphates, as indicators of essential inorganic nutrient materials, were uniformly very low or even apparently absent in the area studied. This seems to be usual in tropical waters. It is discussed in relation to the Great Barrier Reef by Marshall ('33, p. 124). It is not possible to distinguish in the present study the effect of variation of nutrient salts on the plankton growth, with the exception of the area of pollution discussed above.

Most of the species of diatoms, both during periods of great abundance and periods of scarcity, were rather uniformly small in size compared to those of nitrite-rich and phosphate-rich areas, such as, for example, Puget Sound. It would be desirable to make detailed comparisons of the relative sizes of identical species (e.g. *Skeletonema costatum, Rhizosolenia alata,* or *Chaetoceros* spp.) as well as abundance with the concentration of nutrient salts. On the other hand, the small size might be due to the relatively high temperatures of Biscayne Bay and vicinity, or to other factors.

An area of stagnation

The results show that Featherbed Bank (No. 6) and West Elliot Key (No. 7), both located in the southern portion of the Bay, differ from all other stations, in certain important respects. The volume of plankton is uniformly lowest at these stations, the diatom population is of lesser importance, and the dinoflagellate population is of greater importance. Chemical and physical observations show that these two stations tend to be colder in winter and hotter in the summer than the others. In addition, there is a tendency for higher

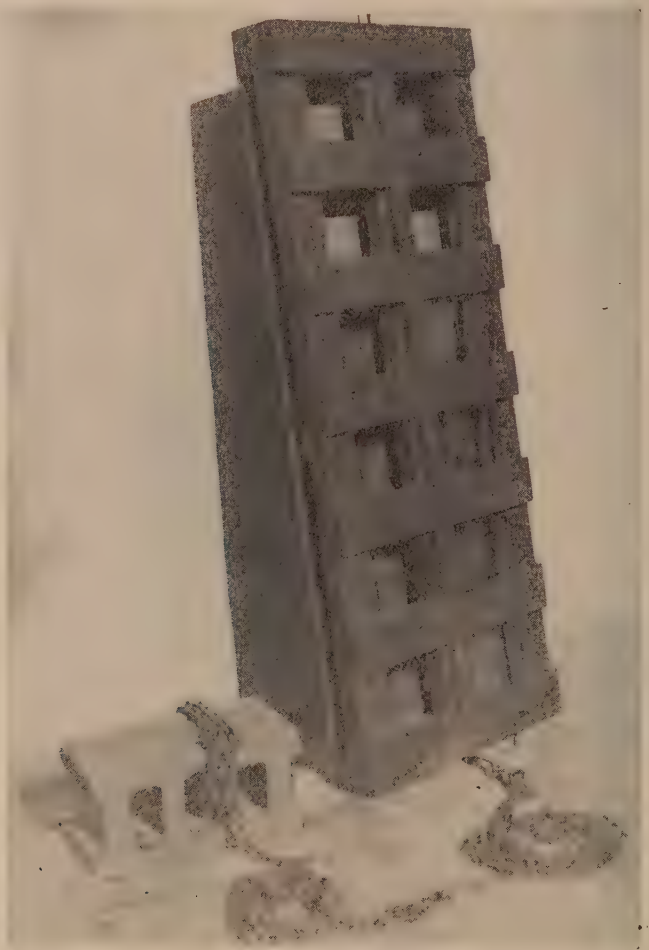

FIG. 2. Raft with slots for glass collecting panels, viewed from beneath. Mooring chain and cement anchor block attached.

salinities, both winter and summer, than at the other stations. On the nautical charts of the area, it may be observed that lower Biscayne Bay, in which these stations lie, is connected directly with the sea only by very narrow and shallow channels, and that it is also cut off to a considerable extent from the more northern reaches of the bay by shallow Featherbed Bank. Thus the water of this portion of the bay suffers a minimum of mixing with any fresh supply of seawater or of water from the upper portions of the bay.

FOULING ORGANISMS

Observations were made at each station upon floating rafts. The rafts were solidly constructed of wood and each one bore on its lower surface twelve slots arranged in two rows (fig. 2). The slots were designed to take horizontal, rectangular glass panels, each 6×8 inches in size.

Experience showed the need for strong ground tackle and the rafts were accordingly anchored by means of $\frac{3}{16}''$ chains provided with swivels and about three

times as long as the depth of the water. The anchor consisted of two heavy concrete, hollow building blocks to which the chain was shackled. In spite of the rugged nature of the anchors, rafts were lost on several occasions, partly by storm damage. It is believed, however, that some of these were stolen, since anchor chains were very scarce during the period of the survey.

When first set out, each raft was provided with one glass panel. At approximately monthly intervals, a new panel was added and the lower surfaces of all the previously inserted panels were examined. In this way, not only was the initial attachment and growth during each month observed, but also the progressive changes in the sessile communities from month to month.

In addition to identification of as many of the species as possible, the number of barnacles and the greatest diameter of the largest barnacle were recorded. The area of the glass panel covered by attached forms was recorded as tenths of the total area. The greatest dimensions of solitary ascidians and branching Bryozoa were also measured. Attempts to obtain the wet weight of each panel were abandoned since it was found impractical to use even a spring balance in a small boat under the weather conditions frequently encountered.

Organisms

Since observations were confined to one type of collector, the organisms encountered were not fully representative of the region, and do not admit of detailed comparison with those of other regions. It was noticed, however, that the forms collected are generally typical of the West Indies, although a few are also encountered at stations as far north as Beaufort, North Carolina. They agree with the list given by Weiss ('48) for the northern part of the bay. The principal organisms appearing on the floats are shown in table XI, which represents the month by month attachments to the panels of each raft.

Slime film, although present on all the rafts, was obscured in many cases by the heavy attachment of macro-organisms and no indication was given in the present series of observations that it is a necessary preliminary to the attachment of the larger forms. On those rafts in the lower bay, which had relatively little fouling, slime was present at all times of the year. Composition of the slime was not subjected to detailed investigation, but in most cases it was brown in color due to diatoms. The thickness of the film varied, and during periods of heavy weather a considerable amount of silt was often present. The silt consisted usually of the fine calcium carbonate or marl, characteristic of this region. It was particularly noticed at the stations in the lower bay and outside Hurricane Harbor. It was never heavy at Trimuph Reef.

Algae were particularly evident in the lower part of the bay and were usually absent to the north, where animals were plentiful. The only exception was a fairly heavy growth of *Enteromorpha* sp. at Station 1 during November. At other stations, *Enteromorpha* was never found. *Acetabularia* and *Batophora* were frequently in evidence. Less common genera were *Dasya, Polysiphonia, Chondria* and *Laurencia.* Algae were found at most times of the year, but were less noticeable during November and December.

Coelenterates were never very plentiful at any of the stations. *Tubularia* was found during December to March, mostly in the lower bay. Other hydroids, unidentified, were noted only on rare occasions.

Bryozoa were represented by *Bugula neritina* and by the encrusting form *Watersipora cucullata. Zoobotryon pellucidum,* which sometimes forms dense, heavy branching masses on piling, was surprisingly rare on the panels. *Bugula* was plentiful, and more marked in the northern part of the bay during November to March. A smaller peak was evi-

dent during May, and again in August. The only noticeable exception to this distribution was a single occurrence at Triumph Reef in April. *Watersipora* was heaviest in the northern part of the bay during December to March, and again in May. It was also fairly frequent in the stations of the lower bay and Triumph Reef, but never in large quantities. The peak periods were from December to March and in May.

Polychaets were never abundant. The calcareous tubes of serpulids were occasionally noticed during April to July. Like other small organisms, they appeared to be unable to compete with the larger forms in the upper part of the bay, but were present in small numbers at the other stations. An interesting form found inside Hurricane Harbor during July was *Dasychone* sp., forming a colony of small parchment tubes.

Mollusca were poorly represented. *Anomia* sp. was occasionally found on the surface of panels when the growth of other organisms was not heavy. It was found much more frequently, however, on other parts of the raft and on the upper surface of the glass panels which did not otherwise appear to encourage larger organisms.

Ostrea virginica occasionally appeared on the rafts, but never on the exposed surface of the panels.

Crustacea were principally represented by *Balanus amphitrite* and *B. improvisus*. These occurred at all times of the year, but principally during November to March, and from May to July. Attachments were much greater in stations of the upper bay, although large attachments occurred at the eastern Elliot Key station during November, and at Chicken Key from November to March. *Balanus eburneus* was freqently found but the remaining balanomorph barnacles of this region, *Tetraclita squamosa* and *Cthamalus stellata,* were almost absent from all stations. *Lepas anatifera* was found at Triumph Reef and in Biscayne Channel in small numbers during May and June, and again in February on the eastern shore of Elliot Key.

The tube living amphipod, *Erichthonius* sp., was found in fair quantity, but only in the stations of the upper bay. It appeared during April to July and again in November. It was not only found on the exposed surface of the panels but frequently in large numbers on the upper sheltered surface as well.

Ascidians were probably the most successful colonizers of panels in the upper bay, but rarely present elsewhere, except at the western side of Elliot Key. They were represented by the large, knobbly, white *Styela plicata* and to somewhat lesser extent by *Ascidia hygomiana, Ascidia nigra* and *Ecteinascidia turbinata.* Attachments took place during all the months of the year, but reached a peak from May to July, and a much smaller peak during March. Colonial tunicates were represented by various brightly colored botryllids, the white encrustation of *Didemnum candidum* and occasionally by mottled growths of *Symplegma viride.* Heavy collections of fouling organisms were sometimes covered by a thin greenish network of *Perophora viridis.*

Colonial tunicates, like the solitary forms, attached throughout the year, peaks occurring during May to July and to a lesser extend during December. Attachments were heaviest in the upper enclosed parts of the bay.

In addition to the organisms listed above, there were occasionally found free living animals which made their homes among the attached growth, although they cannot properly be classified as sedentary organisms. These include numerous crabs, shrimp, young spiny lobsters, amphipods, caprellids and small fishes. Fish eggs which were not identified, and occasionally the eggs of mollusks, were also found attached to the panels. Frequently, on the upper surface of the glass panel, or on the raft itself, there appeared organisms which were not observed on the collecting surface. Most commonly occurring in this category was *Anomia* sp.

Sponges were not found during the survey.

Initial fouling

The organisms observed on each panel at the end of the first month of exposure are listed in table XI. The results of observations are also shown in summarized form in figure 3.

The greatest amount of attachment was observed in the upper bay (Nos. 1, 2). A comparable amount of attachment was also found in the land locked harbor of Biscayne Key (No. 4). Station 3, near to Station 4, but in the open water of the bay, showed distinctly less accumulation of fouling except during the months of February and March. The remaining stations acquired markedly less fouling throughout the year. During the month of May, Triumph Reef (No. 9) showed a greater accumulation than other stations in the southern part of the survey area. East of Elliot Key (No. 8) and at Chicken Key (No. 11), respectively, higher attachments appeared during November and December.

In general the peak of attachments at the northern stations occurred during May and June, with a smaller one in November. Owing to a loss of rafts there is insufficient information about a mid-

TABLE XI. *Summary of initial fouling accumulation*

0–10	Coverage of plate	Alg.	Algae
B	*Balanus*	T.	Colonial Tunicates
A	Solitary Ascidians	S.	Serpulids
Lep.	*Lepas*	D.	*Dasychone*
Bug.	*Bugula*	H.	Hydroids
EB	Encrusting Bryozoans	Amp.	Amphipod tubes

Balanus and *Lepas* by numbers, others by coverage

Station	1	2	3	4	5	6	7	8	9	10	11
April 1945	—	—	1 B:1 EB:1	—	0	—	0–1 T	0	3 B:9 Bug:2 EB:1	0–1 B:2	0–1 EB
May	10 B:400 Bug:1 EB:2 T:6 Amp.	10 B:400 A:10 T:1	1 Alg. S	10 B:20 T:9 A:1	0–1 B:3 Alg.	—	1 T:1 Alg.	1 EB S	1 A Lep. Alg.	1 EB:1	1 B EB
June	10 B:100 T:9 Amp.	10 A:10 B T:2	1 B:20 A:1 T, S	10 B:20 A:1 T:10	0–1 Alg.	—	0–1 T,S	1 Alg.	1 Lep.	1 EB,T	—
July	10 B:50 T:9 S	10 A:10 B T:1	1 T Amp. D	7 B:65 T:4 D:1	0–1 Alg.	—	0–1 Alg.	1 Alg. S	—	0–1 Alg.	—
August	4 B T	—	2 T:2	5 B:70 A:1 Bug:2 T:1 D:2	—	—	—	1 Alg.	—	—	—
Sept. to Oct.	—	—	—	2 A:1 T:1 D:2	7 B:500	—	—	—	—	—	1 B:14 Alg,H

TABLE XI—*Continued*

Station	1	2	3	4	5	6	7	8	9	10	11
Nov.	5 B:2 Bug:5 EB:1 T:2	—	—	7 B:500	1 B:16 EB:1	0–1 B:6	1 B:25 Alg.	7 B:400 EB:1	—	0–1 B:1	9 B:500
Dec.	8 A:1 Bug:3 T:4 H:1	4 B:200 A:1 Bug:2	2 B:200	2 B:250 Bug:1	1 B:15 Lep:2	2 B Alg. EB	2 H Alg.	—	—	0–1 B:3	2 B:150
Jan. 1946	4 B:200 Bug:2 EB:2	—	5 Bug:1 H:4	7 B Bug:7	—	2 Alg. H EB	1 A,T	—	—	3 B:3 Alg. H	0–1 B:35
Feb.	5 B:10 Bug:1 EB:3	—	9 B:500 Bug:1 Amp:1	7 B Bug:3 T:4	0–1 B:4	0–1 Alg.	2 A:1 T:1	1 Lep:1 Alg.	—	1 Alg.	0–1 B H,Alg.
March	6 B:40 Bug:1 EB:3 S	—	2 B:75 Alg:2	10 B A:5 T:4 Bug:4	0–1 B:6	1 Alg.	1 B:10 A:1	1 Alg.	3 EB:1 Alg:3 S	1 Alg.	1 B:250 H,Alg.
April	7 A:2 Bug:1 T:7 Amp.	—	1 B	7 B A:3 Bug:1 T:4 D	2 B:2 Alg:2	1 Alg.	1 T,A	1 Alg.	2 EB,S Alg:2	1 Alg.	0–1 Alg.
May	—	—	1 B:10 Alg.	10 A:1 T:9 Amp. D	1 B:10 Alg:1	1 Alg.	1 Alg. A	1 Alg.	2 Alg:2	1 Alg.	2 B:10 Alg. H:2

winter peak at Station 2, although heavy fouling occurred during May and June. The pattern of mid-summer and mid-winter peaks may be seen in Hurricane Harbor. Station 3, outside the harbor, shows a peak in February and March alone. Of the remaining stations, only Triumph Reef shows a peak during May. Stations 6, 8 and 11 show the mid-winter peak.

The considerable seasonal variations in attachments with major peaks roughly occurring in mid-winter and early summer are substantiated by the observations of Weiss ('48) which were limited however to the upper bay.

Growth rates

Growth rates during the first month following attachment are shown in tables XII and XIII. It was not possible to obtain comparable growth rate determinations of all organisms throughout the year principally owing to the intense competition existing at certain times and to the absence of organisms at others. Further gaps in observations are due to loss of the rafts by storm and human agencies.

With the foregoing reservations in mind, it may be stated that in general the greatest amount of growth following attachment took place during the months be-

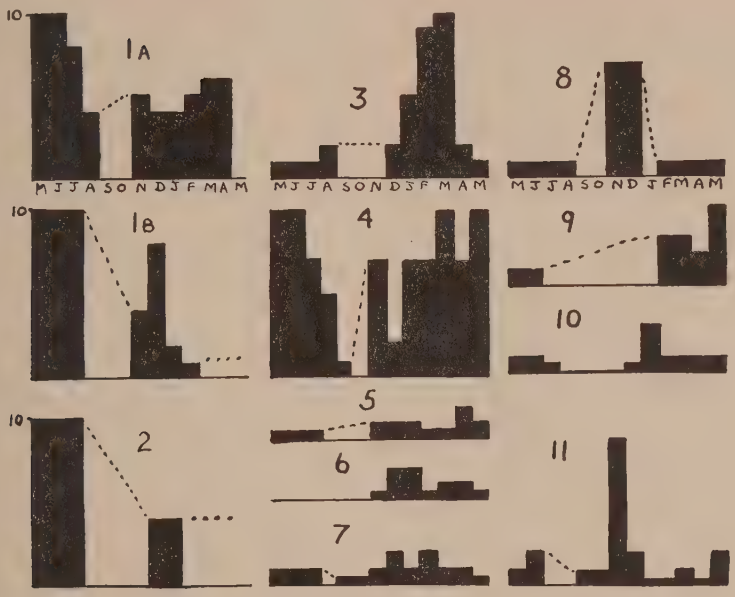

FIG. 3. Monthly fouling accumulations expressed in tenths of panel covered after one month of exposure. Station 1B is in the same locality as station 1A but is inside covered boat slip.

tween April and July. In spite of the fact that during December the lowest sea temperatures were observed, there was also a slight increase in growth rate during mid-winter. Thus, the periods of maximum growth coincide generally with the periods of greatest attachment.

Greatest growth was observed at the stations in the upper bay (Nos. 1, 2, 3, 4). Even during the summer peak, growth at

TABLE XII. *Season of maximum growth*

Figures indicate greatest growth in any direction recorded at each station during the month of attachment, measured in millimeters

Organism	Station											
	1A	1B	2	3	4	5	6	7	8	9	10	11
Balanus sp.	*20* May	8 Dec.	14 May	12 April	*20* May	8 Nov.	4 Dec.	10 April	7 Nov.	10 May	9 Dec.	10 June
Lepas anatifera						*23* Dec.			7 Nov.			
Bugula neritina	5 Dec.	10 Nov.	8 Dec.	25 Feb.	*50* Jan.							
Encrusting Bryozoons	10 Dec.	10 Dec.		*50* Feb.			10 Jan.					
Ascidia nigra	*20* May							18 May				
Styela plicata	20 Apr.		25 June	28 May	*60* Apr.			13 Jan.				

TABLE XIII. *Growth rate of* Balanus amphitrite

Figures indicate greatest increase in diameter recorded during the month of attachment, measured in millimeters

	Station											
	1	2	3	4	5	6	7	8	9	10	11	Max.
April, 1945	—	—	12	—	—	—	10	—	5	2	—	12
May	20	14	—	20	3	—	—	—	10	5	—	20
June	—	—	—	—	—	—	—	3	—	—	10	10
July	—	—	8	10	—	—	—	2	—	—	—	10
August	—	—	—	7	—	—	—	—	—	—	7	7
September	—	—	—	7	—	—	—	—	—	—	7	7
October	—	—	—	10	—	—	—	—	—	—	—	10
November	10	—	—	10	8	4	2	7	—	3	9	10
December	7	2	4	3	3	4	—	—	—	9	2	9
January, 1946	9	—	7	—	—	—	3	—	—	—	4	9
February	5	—	10	—	—	—	—	—	—	4	—	10
March	5	—	—	—	—	4	—	—	—	—	—	5
April	12	—	—	—	—	4	5	—	—	—	—	12
May	—	—	10	—	—	—	10	—	—	4	—	10
Maximum	20	14	12	20	8	4	10	7	10	9	10	20

Stations 5, 9 and 10 was considerably lower than at the others.

The amount of growth recorded for individual species was generally much greater than observed by Edmondson and Ingram ('39) in Kaneohe Bay, Oahu. It was also decidedly greater than at Beaufort, according to the data supplied by McDougall ('43).

Balanus amphitrite during May 1945 showed a maximum increase of diameter of 20 mm. This is considerably in excess of the 15 mm reported by Edmondson and Ingram for a period of forty to sixty days. McDougall records a growth of 12 mm for a four week period.

Bugula neritina attained a maximum length of 50 mm during a four week period in January, 1946. This is more than twice the amount recorded by McDougall. The greatest growth for this species in Hawaii was 25 mm in approximately two weeks.

No direct comparisons are available for encrusting bryozoa. The species *Watersipora cucullata* attained a maximum diameter of 50 mm during the month of February at Station 3. This species was not observed in Hawaii or at Beaufort, but *Schizoporella* grew 30 mm and 45 mm during the same period in these two localities respectively.

Styela plicata at Station 4 attained a maximum length of 60 mm during April This is twice the growth observed at Beaufort and more than four times the rate observed at Kaneohe Bay. Edmondson ('44), however, reports the growth of an unknown species of solitary ascidian at Pearl Harbor. This grew to 50 mm in length during sixty days.

Succession

The organisms initially appearing upon the panels varied with the time of the year and the station as already described. There did not appear to be any regular order of succession. Supplementary observations on microscope slides exposed during March when barnacle attachments were heavy showed that settling would take place in less than two hours after immersion of the glass surface. The presence of a slime film does not, therefore, seem to be necessary for settlement by barnacles. Further observations over the past few years of a similar nature have shown this to be equally true for encrusting bryozoa and colonial tunicates.

The growth on panels subsequent to

their first month of exposure appeared to depend upon the intensity of periodic sets of the various organisms and their ability to survive competition. At the stations where attachments were poor and growth slow, the monthly changes in fouling on the continuously exposed panels were generally in the nature of additions which corresponded to the attachments on initially exposed panels. To some extent the organisms already present tended to die or lose attachment, possibly due to lack of food.

Heavier setting and more vigorous growth produced different effects at stations in the upper bay. Thus, a heavy growth of barnacles during January at Station 1 was gradually overgrown by subsequent sets of encrusting bryozoa and *Bugula*. While this covered the shells of the barnacles, it did not prevent their continued growth. In March and April, however, colonial tunicates developed and, while at first ineffective, these, by the end of April, had greatly reduced the number of barnacles that remained alive. A similar sequence was observed at Station 4. Barnacles were able to survive following attachment of *Bugula*. A heavy growth of solitary ascidians during May, however, finally resulted in the death of all the barnacles, which were completely overgrown.

Encrusting bryozoa were the first to attach during December at Station 1. These were not affected by subsequent growth of barnacles which did not settle upon them in large numbers. By the end of March, however, they had been largely smothered by growth of *Bugula*. By the end of May, solitary ascidians had largely replaced all other forms.

Colonial tunicates which attached during May and June at Station 4 were partially superseded by barnacles and later by solitary ascidians. At this station it was observed that the presence of heavy growths of solitary ascidians prevented further attachment of barnacles, although colonial tunicates and, to some extent, *Bugula* were able to attach. Colonial tunicates, at various times and places, were frequently lost, apparently by mechanical action as a result of poor adhesion. Other organisms prevalent at the time were then able to attach. The solitary ascidians remained for a longer period but eventually were lost in clumps as their weight became excessive and the area exposed to wave action increased. Other organisms then became attached.

Thus there was no regular succession, since all organisms attached at some period of the year during the initial month of exposure, depending upon the intensity of breeding, and were not greatly dependent upon the presence of previously attached organisms. Seasonal succession was present only where earlier arrivals had not taken complete possession or where the later arrivals were able to attach and to exert a smothering effect upon the earlier attachments by virtue of numbers. Breeding appeared to take place to a limited extent at all seasons and the species attaching at any one time and place depended mostly upon the relative breeding intensities at that time and place. Solitary ascidians appeared to be most capable of supplanting others and of resisting further attachments. To this extent they may be regarded as a climax, although even they would sometimes be lost and leave a clear space for others as they open in size. The order in which the remaining organisms were able to supplant each other depended to a considerable extent upon the relative amount of already attached growth and of the intensity of new attachments.

In the case of many of the organisms, breeding, as shown by attachments, continued throughout the year to a varying extent. Similar observations were made by Scheer ('45) at Newport Harbor, California, where the range is very small, 14° C in February to 19° C in July. At Beaufort where the range is from 5° C in February to 28° C in July, McDougall ('43) observed that organisms were decidedly seasonal in their breeding habits. Perhaps as a result of this there ap-

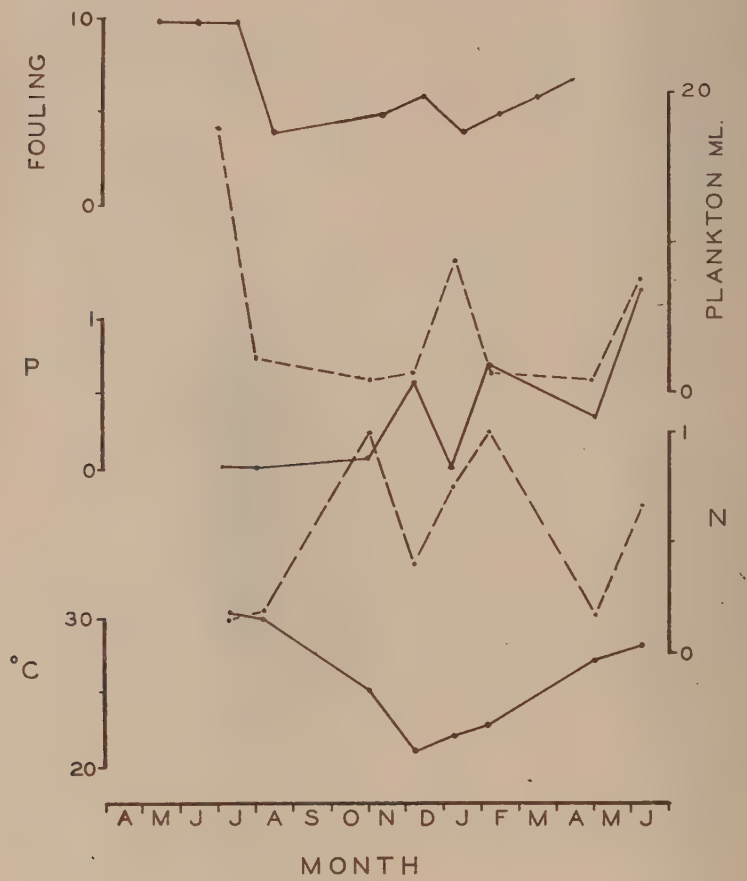

FIG. 4. Average of quantitative observations at stations 1 and 2 in the northern part of Biscayne Bay. N: nitrite nitrogen, P: phosphate phosphorus both expressed in microgram atoms per liter. Fouling expressed in tenths of panel covered after one month of exposure. Plankton expressed in milliliters per standard sample.

peared to be a seasonal progression at Beaufort, whereas at Newport this was greatly overshadowed by an ecological succession. At Miami the temperature range was from 16° C in December to 32° C in July and, although fouling tended to occur at all months of the year, there were decided peaks in intensity. This may be the reason for the lack of any definite ecological succession. On the other hand, succession was not truly seasonal. This may possibly be an indirect result of higher temperatures which would bring about the much greater growth rate of organisms. Thus competition would favor earlier attachments to the extent that organisms in season would not necessarily replace those out of season. Furthermore, there appeared to be considerable variation in the life of attached organisms, some of which only disappeared as a result of mechanical difficulties. The changes in a community of fouling organisms may therefore be regarded as being due to two series of antagonistic factors. The fact of previous attachment, vigorous growth, degree of coverage of surface, and mechanical ad-

vantages such as the bulk and slimy surface of solitary ascidians and length of life are factors favoring the continued attachment of organisms. Intense concentrations of larvae, favorable conditions of food and temperature for rapid growth following attachment, greater efficiency in competition for food and oxygen, such as the smothering of barnacles by a heavy growth of solitary ascidians and the dying out of previous attachments, are factors favoring new attachments. Where physical conditions favor short breeding seasons and relatively brief life and where attachments are light, seasonal progression would be more noticeable. Where breeding is year around as at Newport Harbor, an ecological succession would be observed. At Miami the long breeding seasons and the variability in intensity of attachment and growth rates result in a condition intermediate between a seasonal progression and an ecological succession characterized by considerable variation in the order of succession, but without pronounced seasonal tendencies.

A study of the relative intensity of fouling at the different stations reveals a fairly sharp distinction between those of the relatively enclosed northern part of

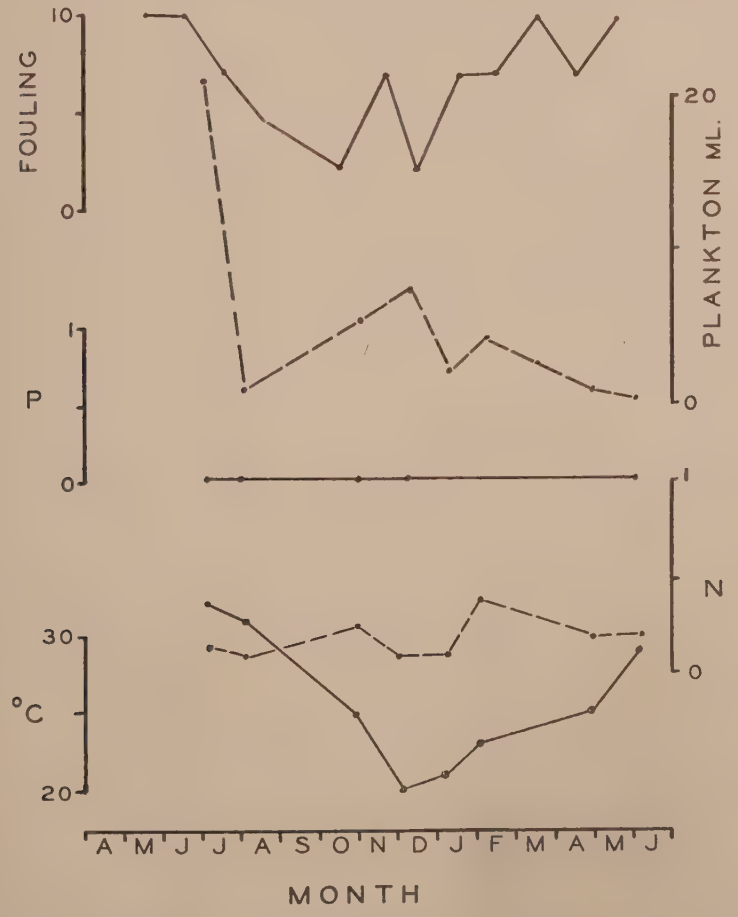

Fig. 5. Quantitative observations at station 4 in Hurricane Harbor. Units as in figure 4

the bay and the remaining stations. Heavy fouling in the upper part of the bay cannot be associated with ordinary land drainage and factors of enclosure alone, since similarly enclosed stations in the southern part of the bay collected very few organisms. The northern part of the bay, however, is rimmed by seawalls and piers which offer a large area for fouling attachment, thereby insuring a plantiful supply of larvae. This is not true in the lower part of the bay where suitable surfaces for attachment are virtually nonexistent, since the shores consist, for the most part, of mangroves. The tidal run of water in the upper bay runs north and south and little mixing taken place. Thus the larvae liberated from the seawalls are not dissipated but remain to bring about re-infection. The upper part of the bay is also heavily polluted with city sewage, resulting in increased nutrient content and plankton growth. These two factors would serve to explain on the one hand the higher intensity of attachment, and on the other hand the higher growth rate characteristic of the upper part of the bay.

Stations 3 and 4, in some respects intermediate in topographical situation, more nearly approximate the northern

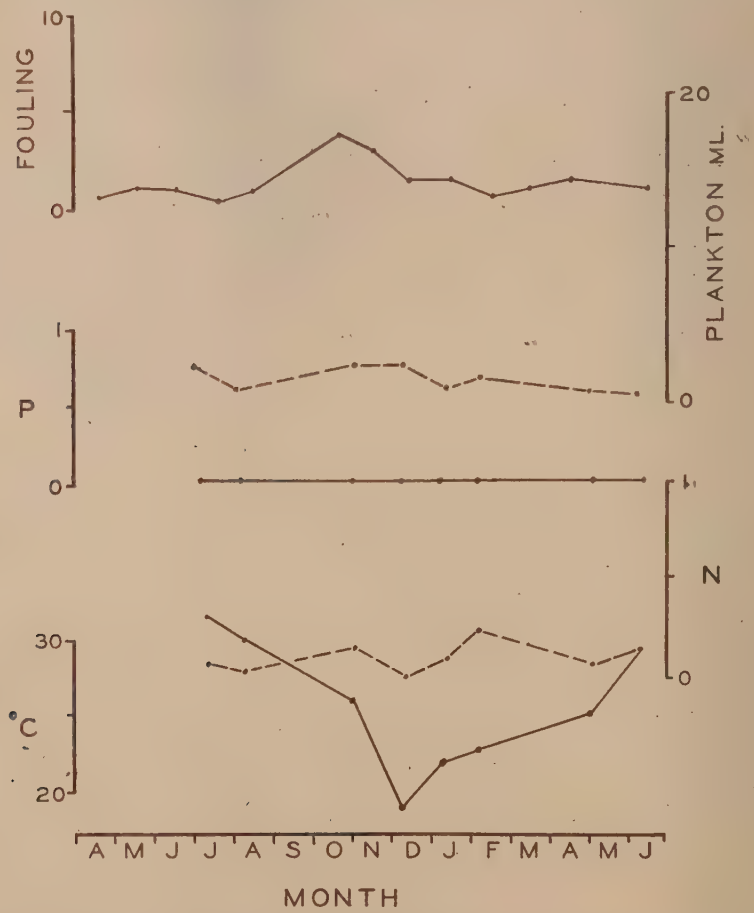

FIG. 6. Average of quantitative observations at stations 5, 6, 7, 10 and 11 in the central and southern part of bay. Units as in figure 4.

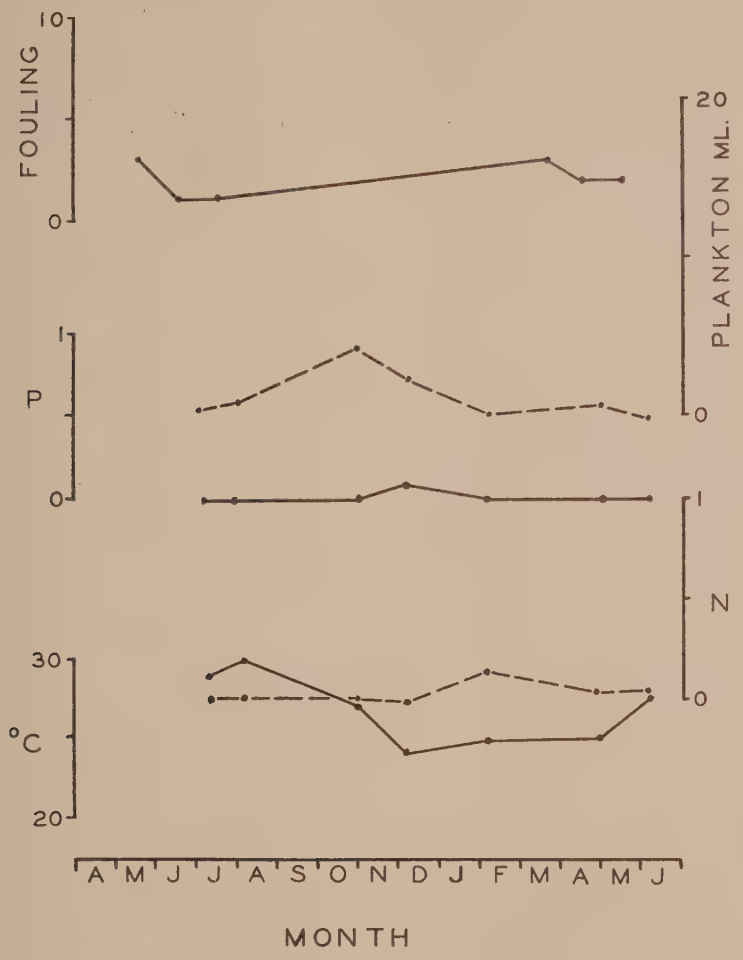

Fig. 7. Quantitative observations at station 9 on Triumph Reef. Units as in figure 4.

stations in their fouling characteristics. Station 3, outside Hurricane Harbor, is noticeably poorer in this respect than the nearby station within Hurricane Harbor. Apparently, the enclosed nature of Hurricane Harbor favors heavy fouling. The lack of mixing with outside water here would also tend to keep larvae in high concentration.

Other stations were uniformly low in fouling intensity. Triumph Reef and East Elliot Key, nearer to the open ocean and Chicken Key, on the inner shore of the middle part of the bay, showed slightly greater fouling than the remainder. These differences and their distribution do not appear to admit of any correlation with the situation of the stations with respect to water currents, land drainage or communication with the open ocean. Stations within and without the bay show no consistent difference.

Summary and Conclusions

In contrast to oceanic conditions which in the tropics are usually rather uniform and which show only slight annual variation, the conditions in Biscayne Bay

exhibited a wide range. Water temperatures ranged 18° C to 32° C in the inshore stations. By contrast, the reef station showed a range of 24° C to 29° C only. Seasonal changes followed, in a general way, the changes in mean air temperature and the total daily hours of sunshine. Variations in salinity were, as might be expected, much greater inshore than offshore. The effects of rainfall and the evaporation of shallow waters during dry summer weather sufficiently account for these ranges.

Dissolved mineral nutrients were extremely low or undetectable at all stations throughout the year, except at a station in the northern part of the Bay where sewage was abundant. It appeared that, in the case of phosphate-phosphorus at least, the plankton growth and nutrient demand were always in excess of the rate of replacement. Unfortunately, it was not feasible to undertake total phosphorus determinations during the survey, but it also appears from the plankton studies that the total phosphorus might also be very low. Nitrite-nitrogen content showed a peak value in February but otherwise followed the pattern of phosphate-phosphorus. The significantly higher nutrient content at the northern inshore stations could well be explained on the basis of bacterial decomposition of sewage components. The greatest plankton concentrations were obtained from sewage polluted stations in the northern part of the bay and in the almost enclosed lake on Biscayne Key. Elsewhere there was little difference between the inshore and offshore stations. Two volume maxima appeared, in July and in December–January. At some of the stations a single peak appeared in October.

While the plankton was generally sparse compared to that of temperature latitudes, the number of species was by no means larger. The higher volumes in the Biscayne Key lake might be attributed to land drainage although this did not appear to be effective on the mangrove fringed shores of the mainland. Inshore areas were quite different in species constitution to the offshore areas.

The generally low phytoplankton volumes are in accordance with the findings of Russell and Coleman ('33) and of Marshall ('34) for the Low Isles areas of the Great Barrier Reef, where it is suggested that the higher metabolic rate of the zooplankton brings about a high grazing rate, thus preventing the phytoplankton from developing any excess of production over utilization.

The organisms attaching to the glass panels suspended beneath rafts were predominantly barnacles, colonial tunicates, solitary ascidians, encrusting bryozoans and *Bugula*. Some organisms of each group attached during every month of the year, but the peak of attachment density occurred during mid-winter and mid-summer. Under the more truly tropical conditions of the Great Barrier Reef, Stephenson ('34) found a similar situation with a slight majority of organisms exhibiting a summer breeding peak only. Growth rates were much higher than previously recorded for the same or similar species, with maximum growth occurring in mid-winter or early summer.

The stations where greatest amount of initial attachment and greatest subsequent growth occurred were in the northern part of Biscayne Bay. This high rate of attachment may be due to conditions favorable to larval growth and development, arising from sewage products, to the continuous harbor works covered with fouling organisms which provide a considerable supply of larvae, and to the relative isolation of the water. Enhanced growth in this area is almost certainly correlated with sewage and enhanced plankton production. Similar conditions of growth and attachment were found in the landlocked harbor on Biscayne Key. The remaining areas, however, showed very poor fouling characteristics. This might be partly due to lack of larvae,

resulting from the absence of rocky shores or harbor works which might support breeding organisms but it is certainly partly accounted for by the lack of nutrients and plankton. No significant difference appeared between offshore and inshore stations in this respect.

The nature of changes in the fouling communities subsequent to the initial month of exposure showed that neither a true ecological succession nor a definite seasonal progression is present. The changes appear to depend upon the relative potency of such factors as concentration of larvae, growth rate, length of life and length of breeding season. The interaction of these factors may reverse the succession more commonly present and may also greatly modify seasonal progression. It was noticeable that solitary ascidians with a high growth rate and large bulk, once established, tended to survive longer than other organisms, yet if attaching in large enough numbers colonial tunicates might completely invest the ascidians and kill them off, leaving the plate once more free for barnacles or bryozoans to colonize. While *Lepas* was more obvious at the reef station it was no less prevalent in initial attachments at the inshore stations. Its presence was obscured by the greater growth of other organisms.

In general, the results indicate the great part played by land drainage and sewage in the growth of plankton and of sedentary organisms, the otherwise low nutrient and plankton content of inshore waters, and the presence of a winter as well as a summer peak in breeding and growth. They also indicate a year around plankton growth limited by the rate of phosphate production and a grazing rate limited by phytoplankton formation.

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NOTES AND COMMENT

THE EFFECT OF LEAF TEMPERATURE ON TRANSPIRATION

The vapor pressure gradient between the air and an evaporating surface is the most important factor influencing the rate of evaporation. The same factor is important in determining the transpiration of a leaf, though physiological and structural features are also influential (Seybold, '29). The opinion that the gradient between leaf and air temperatures has a marked effect on the vapor-pressure gradient between leaf and air, and thus on transpiration, has been advanced by a number of investigators. In particular, Curtis ('36) demonstrated that raising the leaf temperature above that of the air markedly influenced the vapor pressure gradient. These investigators, however, base their conclusions chiefly on theoretical assumptions, unsupported by measurements or experiments in the natural habitat. Consequently their views are not generally accepted by ecologists studying the water balance of plants. But when the factor of the temperature gradient between leaf and air is not considered, serious error in the interpretation of transpiration curves may result. We have therefore considered it worthwhile to summarize the results of experiments which we have carried out in this field on maquis plants growing in the University Botanical Gardens on Mount Scopus in Jerusalem.

Experiments

In order to ascertain the dependence of transpiration upon the temperature gradient between air and leaf, we measured the transpiration rates of identical leaves with varying temperature increments ("temperature increment" is the difference between atmospheric temperature and that of the leaf). Transpiration rates were determined by the rapid weighing of detached leaves on a torsion balance, as described by Huber ('27), the period of exposure being 2.5 minutes. Half a minute before the termination of exposure, the leaf temperature was measured thermoelectrically according to a field method described elsewhere by the author (Konis, '46). Varying temperatures were induced in adjacent leaves of approximately equivalent area and weight by varying their positions so that they were either horizontal or vertical while their transpiration was being measured. We based this method on the fact (Konis, '43) that the temperature increment of a horizontal leaf in the subtropical zone, at noon, during the summer months is many degrees higher than that of a vertical leaf, since a horizontal leaf under such conditions is nearly perpendicular to the sun's rays.

All of our observations were done during the noon hours of June and July, on calm or still days. The results are summarized in table I, which correlates the degree of transpiration with the temperature increments of horizontal and vertical leaves of maquis plants. Each figure represents the mean value of 10 determinations on each of 15 days. Transpiration and temperature observations on leaves in the two positions were recorded simultaneously.

The marked influence of the temperature increment of a leaf on its rate of transpiration is demonstrated in table I.

The temperature increments of the leaves of marquis plants on a clear summer day are capable of increasing transpiration by as much as 30 to 230 per cent. A high degree of correlation exists between the increase in transpiration and the temperature increment of different plants.

It is particularly necessary to emphasize the marked influence of the leaf's position on its rate of transpiration in the subtropical zone. Maximal transpiration rates occur in horizontal leaves and any deflection from the horizontal leads to decreased transpiration. Greatest decreases occur in vertical leaves, in which the smallest temperature increments are to be observed. Seybold ('27), working in the laboratory under controlled conditions, observed maximal rates of transpiration in vertical leaves. In his study all the factors, except leaf position, were identical, including the temperature. However, under certain conditions in nature in the subtropical zone, it is rather the horizontal position that is associated with maximal transpiration. We chose to study transpiration in leaves in varying positions in order to stress the importance of leaf position on the water balance of a plant. In this connection, the great variety of plants with vertical or near-vertical leaves in sunny habitats can be associated with both the heat and water balance.

Conclusions

The results of these experiments permit us to draw certain conclusions about the study of transpiration and the methods by which it is measured, some of which are listed below:

(1) In transpiration studies in the natural habitat observations on the temperature of a plant should be included among the other data recorded, such as stomatal movement, water content of the plant, its osmotic value, etc.; otherwise interpretation of the transpiration curves is likely to be misleading.

(2) The effect of radiation on increase of the transpiration rate (Martin, '35, and others) may

TABLE I. *The effect of the position and the temperature increment of leaves on their transpiration rates*

	a	b	c	d	e	f
Rhamnus alaternus L.	2.5	0.75	8.7	1.4	233	7.3
Laurus nobilis L.	2.0	0.85	7.9	2.1	135	5.8
Arbutus andrachne L.	6.6	4.0	7.5	1.5	65	6.0
Quercus calliprinos L.	9.75	5.2	6.3	1.1	88	5.2
Cercis siliquastrum L.	17.1	8.1	5.0	0.8	111	4.2
Spartium junceum L.	18.0	12.5	4.5	1.2	44	3.3
Pistacia palaestina Boiss.	23.5	18.0	4.2	0.7	30	3.5

a. Transpiration rate in the horizontal position (mg/dcm²/min).
b. Transpiration rate in the vertical position (mg/dcm²/min).
c. Temperature increment of leaf in horizontal position (°C).
d. Temperature increment of leaf in vertical position (°C).
e. The difference between transpiration in horizontal and vertical positions expressed as a percentage of transpiration in the vertical position.
f. The difference between temperature increments of leaves in horizontal and vertical positions (°C).

largely be attributed to the increased temperature increment induced by the radiation.

(3) The marked changes in transpiration rates frequently mentioned in the literature as occurring very rapidly following clouding over of the sun, are to be attributed principally to temperature changes in the leaves. This, at any rate, is the situation in plants whose stomata move slowly, such as those of maquis plants.

(4) The fact that transpiration rates are very low on cloudy days is partially due to the lack of temperature increment observed at such times, as well as to stomatal closure and other factors.

(5) When transpiration is measured by means of rapid determinations of the weight of detached portions of a plant, the leaf should not be exposed to the sun in any accidental positions, as has hitherto been the practice. It should be placed at a specific angle to the sun's rays. The angle chosen should be that assumed by most of the plant's leaves in their natural positions. In any case, it is essential to specify the angle of exposure together with the rest of the data. Only then will the result be comparable.

(6) The transpiration rates of the separate leaves of a plant differ, due, in large part, to the fact that appreciable differences exist between their temperature increments. This, in turn, depends on their varying angles of exposure to the sun's rays, on their position in the plant (whether peripheral or central), and on their varying exposures. For this reason we are unable to predict the transpiration of an entire plant on the basis of observations on a few single leaves, particularly where trees are concerned.

(7) The temperatures of leaves in the direct sunlight are given to marked and rapid fluctuations as a result of various factors such as changes in radiation intensity and in wind velocity. In consequence, transpiration rates will undergo rapid variations, as evidenced by the experiments described in the present paper. Therefore, in order to avoid error in determining transpiration rates by the rapid weighing technique, it is necessary to conduct as extensive a series of parallel experiments as possible, and to extract a mean value from these data, since single observations are unreliable.

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A RAPID METHOD OF SEPARATING SEED OF CHAMISE (*ADENOSTOMA FASCICULATUM*) FROM THE DUFF

In a recent study on the germination of chamise seed it was necessary to obtain large quantities of seed which had lain in the duff for several years. This seed was small enough to pass through a 2 millimeter screen but was retained on a 1 millimeter screen. Unfortunately, so were many of the leaves, twigs, and sand particles making up the duff. Separation by various methods of screening and floating were tested, but proved unsuccessful. Furthermore, since the number of good seed (seed with viable embryos) averaged only 1 per cent of the total, hand separation under 10 power magnification was impractical—10,000 seeds would require handling to obtain only 100 good seed.

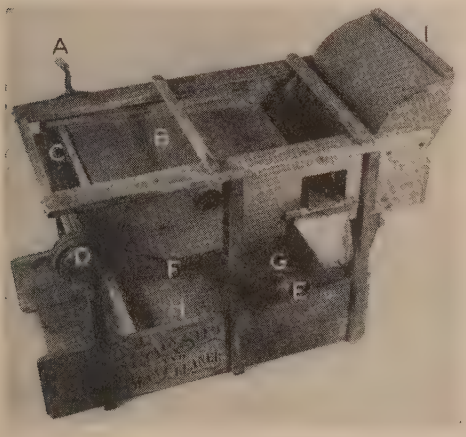

FIG. 1. Clipper seed separator. A, crank handle. B, top screen. C, bottom screen. D, pulley. E, pulley. F, belt. G, fan. H, collecting box. I, opening from fan.

After many attempts a successful procedure was worked out in which use was made of a small hand operated "Clipper" seed separator (fig. 1), which costs about $85.00, and may be purchased from A. T. Ferrell, Saginaw, Michigan, or Walter Steele, 41 Drum St., San Francisco. This machine was small enough to be readily moved into the field where it was set up in a stand of chamise. The surrounding ground was scraped to a depth of approximately 1 inch and these scrapings fed directly on to the top screen (B); the hopper had been removed because it was too easily clogged by twigs and grass. A number 16 top screen (B) and a number 20 lower screen (C) were used.

For the first screening the gear ratio was so adjusted, by use of the belt (F) and pulleys (D) and (E), that fan (G) was rotating at its maximum speed; the material blown out of (I) was saved for the next screening. The second screening was run with the gear ratio adjusted so as to rotate fan (G) at its minimum speed; this time the material falling in box (H) was saved for the next screening. An intermediate fan speed was used for the third screening; both the material blown out of (I) and that falling in box (H) were saved. The material blown out of (I) was rescreened several times until very little would fall into box (H). All the material which had fallen into box (H), from the third screening on, was combined. This material consisted of a high concentration of seed with only a small mixture of leaves.

The seed thus obtained was further cleaned by placing the seed at one end of a shallow box which had been lined with a desk blotter. The box was then tilted at an angle of approximately 45° and the sides lightly tapped. The seed being relatively round rolled rapidly to the bottom where it was removed. The leaves and twigs moved down the blotter at a much slower rate. This process was repeated over and over until all the seed was removed.

This method of separation proved highly successful and plans are now under way to use it for the removal of still smaller seeds.

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NOTES ON THE INHABITANTS OF CERTAIN SPONGES AT BIMINI

During October, 1948 several sponges were examined for microscopic consorts. They were cut into thin sections, like slices of bread, in a metal tub. After all the animals had been picked out the remaining water and debris were strained through a fine sieve. Five species were studied. Two of these were big "loggerheads." Most of the guests were undoubtedly inside, but when only one or two individuals occurred they may have been on the exterior. The large canals in some species of sponges commonly harbor many animals. All specimens came from

the sound east of the Lerner Laboratory. They were collected at depths of 1–2 meters.

My thanks are due to Dr. C. M. Breder, the Director, and to the resident staff of the Lerner Marine Laboratory for the opportunity and for assistance given at Bimini. Dr. Fenner Chace, of the United States National Museum, identified most of the decapod crustaceans; Dr. John T. Nichols, of the American Museum of Natural History, named the fishes; Dr. Olga Hartman, of the Alan Hancock Foundation, named the annelids; Austin H. Clark and Harald A. Rehder, of the U. S. National Museum, the echinoderms and molluscs. The sponges were identified by the writer from de Laubenfels' ('36) account of the sponges of Dry Tortugas. All specimens, except two anemones, have been deposited in the United States National Museum.

Hiricina strobilina (Lamarck)

Three good-sized individuals were examined on October 13, 15, and 19. Their volumes were approximately 50,750, 71,250, and 81,250 cc. These sponges contained 13 fishes: 8 *Risor binghami* (Parr), 3 *Gobiesox macrophthalmus* Gunther, 1 *Auchenopterus* sp., and 1 head of a clinid blenny. There were also 71 alpheid shrimps: 39 *Synalpheus brevicarpus* (Herrick), 31 *S. minus* (Say), and 1 *S.* sp. Thirteen other decapods included 1 *Crangon floridanus* (Kingsley), 2 *C. formosus* (Gibbes), 1 *C. ornatus* (Rathbun), 1 *Processa* sp., 1 *Microphrys bicornutus* (Latreille), 2 *Heteractaea ceratopus* (Stimpson), 2 *Gnathophyllum americanus* Guerin, and 1 *Micropanope nuttingi* (Rathbun), and 1 *Clibanarius* sp. Two stomatopods, *Ganodactylus oerstedii* Hansen, were also present. There were 2 amphipods: *Leucothöe commensalis* Haswell.

The 82 annelids were classified by Dr. Hartman as follows: *Sthenelais setosa* Bush, *Eunice filamentosa* Grube, *Marphysa sanguinea* (Montagu), *Lumbrinereis latrelli* Andouin & Edwards, *Cirriformia tortugaensis* (Angener), *Armandia maculatc* (Webster), *Stylarioides plumosa* (Müller), *Dasybranchus lunulatus* Ehlers, *Terebella magnifica* Webster, *Trypanopsyllis* sp., and an unidentifiable fragment of a harmothoid.

In these three sponges there were also 2 anemones, 40 small rugose clams (*Papyridea semisulcatum* Gray), single representatives of four other clams (*Isognomon listeri* Hanley, *Pinctada radiata* Leach, *Lima antillensis* Dall, *Cumingia coarctata* Sowerby), a snail (*Cypraea cinerea* Gmelin), a small brown mottled holothurian, 94 ophiuroids (2 *Ophiothrix oerstedii* Lütken, 3 *Ophiactis müller* Lütken, 40 *O. savignyi* (Müller & Troschel), 1 *Ophiocoma pumila* Lütken, and 1 *Ophioderma cinera* Müller & Troschel) and 3 sea urchins *Eucidaris tribuloides* (Lamarck).

A small sponge of this species (vol., 7,700 cc.), collected on October 13, contained only one ophiuroid.

Speciospongia vesparia (Lamarck) Marshall

Two specimens, collected on October 30, had volumes of approximately 15,660 and 10,080 cc. These were much smaller than those studied by the writer (1932) at Tortugas. They contained 415 alpheid shrimps: 156 *Synalpheus brooksi* Coutière, 53 *S. longicarpus* (Herrick), 20 *S. pectiniger* Coutière, and 2 *S. rathbunae* Coutière. There were also 13 shrimps: *Periclimenes* sp., 2 *Crangon normani* (Kingsley), and 10 *C. cylindricus* (Kingsley), and 2 crabs; *Tipton tortugae* Schmitt and *Processa* sp.

The alpheids harbored bopyrid isopods: 8 female and 4 male *Hemiarthrus schmitti* Pearse, and 2 female and 1 male *Bopyro choprae* Pearse.

Aulospongus schoemus de Laubenfels

A single individual of this branching sponge was examined on October 20. It contained a crab, *Processa* sp., and 2 annelids.

Iotrochota brotulata (Higgin) Ridley

An individual of this branching brown sponge collected on October 29 contained 2 alpheids, *Synalpheus* sp., and a shrimp *Periclimenes americanus* (Kingsley), 3 annelids, and a cidaroid sea urchin.

Haliclona rubens (Duchassaing & Michelotti) de Laubenfels

Four of these red sponges were examined on October 22 and 29. They ranged from 9,000 to 20,000 cc. in volume. They contained a total of 4 alpheids, *Synalpheus brevicarpus* (Herrick); a shrimp, *Periclimenes* sp.; and 5 crabs: 2 *Panopeus herbstii* Milne-Edwards, 1 *Tipton* sp., 1 *Porcellana sayana* (Leach), and a *Macroceloma trispinosum* (Latreille). There were also 2 stomatopods, *Gonodactylus oerstedii* Hansen, and five amphipods: 4 *Leucothothoe commensalis* Haswell, and an unidentified red species.

In addition to these crustaceans there was a fish, *Pomacentrus leucostictus* (Müller & Troschel), 2 small clams, 7 snails (*Pustularca adamsi* Smith), 1 annelid, 1 anemone, 1 holothurian, and 6 ophiuroids.

Discussion and Summary

The two loggerheads at Bimini had fewer consorts than those studied by the writer ('32) at Dry Tortugas. There 3 specimens of *Speciospongia vespara* contained 0.09, 0.13, and 0.27 animals per cc. of body volume; whereas at Bimini the same sponges averaged only 0.035 per cc. Another sponge, *Hiricina strobi-*

lina, at Bimini, though larger in size, made a worse showing, with 0.0047 animals per cc. *Hiricina* had a greater variety of guests—fishes, alpheids, crabs, shrimps, stomatopods, annelids, anemones, clams, ophiuroids, and echinoids. *Speciospongia* had a higher number of animals per cc. mostly because of its large number (415) of alpheid shrimps and their bopyrid parasites. It had no amphipods, stomatopods, annelids, clams, ophiuroids, echinoids, or anemones.

The sponges at Bimini come from a shallow enclosed sound; one of those at Tortugas was collected at a greater depth and all were from the open ocean. The Bimini sponges showed marked individual differences in their contained faunas. The loggerheaads at Bimini also differed from those studied at Tortugas in their greater variety of fishes. The only fish encountered at the latter locality was *Evermanichthys metzelaari* Hubbs. There was a barnacle in the Tortugas sponges and none at Bimini. None of the eleven species of annelids at Bimini was the same as any species at Tortugas.

The number of animals that live in sponges apparently varies with locality and habitat. Small dense sponges have few or no consortes. Large individuals with good sized internal canals may serve as veritable living hotels. At Tortugas loggerheads from deep water contained more animals than those from lesser depths.

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TAXONOMY AND ECOLOGY

In a recent issue of Ecology, Dr. A. G. Huntsman ('48) introduced a discussion of "Method in Ecology—Biapocrisis" with the following statement: "Ecology is the study of organisms, made in the places where they live rather than in the museum or in the laboratory. When one knows the kinds (*the extensive museum and laboratory work of the past makes this readily possible*), one is next concerned with the distribution and abundance of each kind." (Italics mine.)

While this acknowledgment of the debt of the ecologist to the taxonomist is well intended and will be appreciated by taxonomists, the statement will be considered truly remarkable by students of many groups of invertebrates, especially insects.

Generally speaking, at least in this country and with reference to zoology, it is only in groups of relatively few and well-known species (mammals), in groups that have long attracted the attention of collectors and naturalists as well as of specialists (birds, butterflies), or in groups of economic importance or public health significance (fruit flies, mosquitoes), that there is even a reasonable facsimile of the Utopian situation postulated by Dr. Huntsman. Ecologists whose problems and conclusions involve and depend upon systematic zoology, especially in most groups of arthropods, need bear this particularly in mind. The point may be considered of special significance in insects, for the abundance and ubiquity of these animals mean that they are frequently and easily collected in the considerable numbers that lend themselves to comparative ecological studies.

There are surprisingly few groups of insects in which the classification is so well worked out at the specific level, and well enough presented in published works, that ordinary determinations can be depended upon. This is especially true in those insects whose small size, inconspicuousness, or unattractiveness has caused them to be neglected. In many such groups, no comprehensive revisions have been carried out for decades, or none since greater attention has been paid to characters of the male and female terminalia.

In all too many cases we are still merely quoting the names and conclusions of workers of the last generation, or even earlier, because there has been no one available to study the groups in the light of modern techniques and concepts. When they are studied, we often find that old records of "common species" mask a whole complex of forms.

A few examples will suffice for illustration. Ross ('37) in the neuropteran genus *Sialis* (alder flies) recognized a number of new species with this comment: "Critical study of the genitalia has revealed no less than ten eastern and six western species grouped under the name *infumata.*" Oman ('33), who studied the important economic group of agallian leafhoppers, recognized in one part of the genus *Aceratagallia* a total of 26 species that had previously been placed under five names, besides considerable confusion among these five in their proper application. Shewell ('39) revised the dipterous genus *Camptoprosopella,* a genus of small yellowish flies commonly collected on grasses and other low vegetation, and described twelve new

species, most of which had been recorded for years under the name *C. vulgaris* (Fitch), a species which, incidentally, could not even be recognized with certainty because the type is a female. The present writer ('49) found twelve new species, with characteristic terminalia in both sexes, in what had been widely determined for many years as a common Holarctic species, *Leptocera lutosa* (Fallén) (Diptera). In the abundant and persistently annoying eye gnats or *Hippelates* flies, which have been of some interest as vectors of yaws and various eye diseases, the writer has found no less than nine distinct species of three genera standing in collections under the name *Hippelates pallipes* (Loew), in this case all named species whose correct recognition requires painstaking attention to minute details.

Needless to say, in such animal groups "knowing the kinds" has approached being "readily possible" only within the last few years. In many groups, the lack of adequate support for taxonomic work and the relatively few students entering the field, among other factors, postpone indefinitely the time when careful and comprehensive studies can be carried out. The situation is particularly intriguing, for it is contemporaneous with the great interest in such fields as evolution, zoogeography, and speciation, which depend so greatly for their raw materials on the data published by the taxonomists!

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HERMIT CRABS IN FOSSIL SNAIL SHELLS IN BERMUDA

A very conspicuous inhabitant of all the West Indies, from the Bahamas in the north to Dominica in the south, and of the coast line of North, Central and South America from Key West, Florida to Brazil is a large terrestrial hermit crab which indeed has become so independent of the ocean that it is often seen far away from the beaches and even high up on hills. The name of this rather aberrant crustacean is *Cenobita diogenes* Latreille. Like all hermit crabs, this species shelters its soft abdomen in snail shells. In accordance with its stately size, only large snail shells can serve this purpose. In all the localities of its wide distribution, the crab is mostly seen carrying around the heavy, trochoid shell *Livona pica* Linnaeus, which is very abundant throughout that area.

In Bermuda, the aptly named *Cenobita diogenes* is still abundant though at the northern limit of its range. There are no fresh *Livona* shells in Bermuda to serve as hermit-crab houses; but fortunately for our hermit, the Pleistocene and even more recently extinct *Livona* left abundant fossil and subfossil shells in the aeolian sandstone deposits that compose the higher ground of the Bermudas. These are excavated by the hermit crab, and used quite in the same way as are the more recent shells elsewhere. Without this supply of large shells, there would not be nearly enough large snail shells for the Cenobitas of Bermuda.

The marine shell *Livona* flourished in Bermuda waters and apparently became extinct there in glacial times. *Cenobita diogenes* also lived on the Bermuda beaches in preglacial times, and used the *Livona* shells to house its soft abdomen then as now. In fact, the abundance of fossil *Livona* shells in the Bermuda sandstone can only be accounted for by the fact that the hermit crabs carried the shells up to all levels while the sands were being blown up and deposited by the winds of the glacial era.

Thus the Cenobitas survived the extinction of their house-producer because the activities of their own ancestors had laid up a store of solid shells.

Everywhere in Bermuda one sees the hermit crabs with their *Livona* shells, small and large according to age, in gardens, and on the heath-covered hillsides. There are abundant empty *Livona* shells scattered about, and there can be no doubt that one and the same shell has often served as house for long successions of hermit inhabitants.

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BOOK REVIEWS

Principles of Animal Ecology—An Appraisal [1]

Teachers and students concerned with the rapidly maturing field of ecology have long been painfully aware of the absence of books covering the range of subjects encompassed by the ecological journals. Consequently, when five distinguished ecologists, representing diverse specialities, devote some 50 man-years to compiling a book designed to delimit the field, the result can scarcely fail to have a momentous influence in directing the future course of developments in ecological thought.

In their advertising the publishers refer to this book as "without any question the definitive work in the field," a statement with which the reviewer is pleased to express unqualified agreement. No obvious phase of ecology, as understood by biologists, has been slighted. Nowhere else in a single volume can one find such a treatment of organisms as genetic systems, functioning in populations and taxonomic categories, inextricably united by ultimate interests with other organisms and groups, and at each level from the gene through the many-species system functioning as a unit in relationship to a multi-faceted environment.

But we have been in need of several books on ecology. In the preface the authors recognize three demands: for an encyclopedic treatise of present-day knowledge, for a brief statement of underlying principles, and for a study of these principles together with a sampling of the supporting evidence—and to this list the reviewer would add a *textbook* with the aid of which a reader might learn some principles while coasting along on narrative-type presentations of evidence and in which the student might find some directions for procedures in ecological studies. It is the third of the above needs which the authors have undertaken to fulfill, but quite possibly they have also satisfied any demand for a treatise of the first category. Textbook needs were apparently not considered—an emphatic observation by the reviewer who chose this volume as a text even before it came off of the press. The advertising misleads in implying that elementary biology students can understand a large part of this book. On a percentage basis the claim might be justified, but pedagogically it is desirable to have a number of consecutive pages understandable and it may be stated on empirical grounds that a very limited number of such sequences can be found in this volume. However, it is unjust to criticize a book for not being something it was never intended to be and we must turn to an appraisal of the actual contribution.

The book is replete with examples drawn from a ubiquitous literature which is assembled in a 70-page combined bibliography and author index of inestimable value, a feature which alone would make the volume indispensable to professional ecologists. The examples have been selected with such extraordinary care that it is almost impossible to question the validity of facts anywhere in this work. Curiously enough Dallinger's incredible results on temperature acclimatization are described without comment (p. 22), and the reviewer must express reservations regarding the relationships of human efficiency to climate (p. 110, 208–209) and the lifting power of warm air within the air sacs of birds (p. 132). Nevertheless, this book probably establishes a new high standard of factual accuracy for any work of such scope. Also noteworthy, while discussing the bibliography, is the admirable policy of frequently citing sources of opinions contrary to those maintained by the authors.

Written by five zoologists and including the word "animal" in the title this book might have been expected to perpetuate the illogical cleavage of ecological subject matter along taxonomic lines but, happily, this is not the case. Examples drawn from zoological studies predominate, but the place of plants in relationship to principles is nowhere ignored. The reviewer would have deleted the word "animal" from the title.

The introduction is followed by a highly condensed 60 page history of ecology extending to *ca.* 1940 which is noteworthy for its thoroughness in summarizing a field never before adequately summarized rather than for its qualifications as light reading matter. It would be presumptuous to attempt any critique of this section without first duplicating the vast amount of scholarly study known to have gone into its preparation. The reviewer merely expresses surprise that Humboldt does not loom larger and that Schimper is not even mentioned (except much later in a reference given on p. 582 and omitted from the bibliography). The section ends with a four-page appendix listing ecological periodicals, journals containing ecological material, and references to important books and review articles published between 1931 and 1942. This is a duplication of material in the bibliography and is a slightly incongruous element in a work where "a short chapter on electricity as an environmental factor has been omitted to save space" (p. 157).

[1] **W. C. Allee, A. E. Emerson, Orlando Park, Thomas Park, and Karl P. Schmidt.** Principles of Animal Ecology. W. B. Saunders Co., 1949. Pp. xii + 837, 262 Figs. $14.

Section II entitled "Analysis of the environment" consists of 14 chapters in 154 pages dealing with the physico-chemical environment and autecology. Reading this section one senses (and this is more than a personal opinion of the reviewer) a certain restraint, a resolve to describe the physical environment while suppressing the more savory and better understood biotic data. A physical scientist might have condensed this section both by generalization and deletion. For example, many of the effects of pressure discussed on pp. 136–137 are inherent in Le Chatelier's rule to which separate space is devoted on p. 138. Perhaps the authors are less ready than the reviewer to accept this rule, as well as a knowledge of molar and normal solutions (p. 167), the pH scale (p. 172), and similar matters as part of the common knowledge of present-day undergraduate science students. On the other hand, some formulas, such as that for the penetration of light into water (p. 124), are presented without sufficient discussion to make them of any conceivable use to the reader or, as in the case of the "ecological radiation unit" (p. 91), without any evidence that there is a justifiable reason for using the measure. However, when one has left the physics of each chapter and come to the animals the material is absorbing, well-chosen and well-described—although frequently with somewhat complex terminology.

Beginning on p. 236 under the heading "Impact of food surplus" the reader experiences the relief of finding the authors on their home grounds and proceeding convincingly. At this point the postulate: "It seems to be a fundamental attribute of living organisms to tend to use all available food supplies" is set forth, and on this base the evolutionary expansion of life into new habitats and the basic nature of the biotic environment are skillfully and meaningfully developed. The reviewer would have liked to have seen this concept expanded to include as a general organic attribute the tendency to occupy all available niches (using this term for any combination of the possible means of obtaining a living from a given environment). Such an approach might have simplified some of the later discussion, for "adaptive convergence" (p. 668) could have been equated with niche-filling, "preadaptation" (p. 642) could have been discussed in a less extreme sense as a tendency for selection to operate on genetic differences within a superfluity of offspring and with a tendency to perpetuate abilities to fill unoccupied niches, and much of the evolutionary discussion as well as the phenomena of adaptive radiation could have been brought within the limits of a single principle.

The third main section of the book consists of seven chapters in 173 pages dealing with populations. The first four of these chapters constitute about as excellent a general discussion of populations as could conceivably have been squeezed into the space. Beginning with the biological backgrounds of natality, mortality, age-distribution, and dispersion, population phenomena of ecological importance are developed and illustrated in a meaningful manner which for the first time brings this important subject matter within the reach of many students of ecology.

Coming to Chapter 22, "Population factors and selected population problems," we may pause to note a feature of the book which bothered the reviewer in several places. Preoccupied with "principles" (definable in their sense as generalizations from facts which assort facts in meaningful order) the authors have tended in some cases to select and advocate a principle, and to force the sometimes reluctant data into harmony with it, and have then proceeded to confuse the reader by pointing out the exceptions and complications created by adopting the principle. This could be illustrated with respect to "bonitation" (p. 209), the "principle of partial equivalence of different ecological factors" (p. 223) or some of the material falling within the vacillating definition of the community (cf. p. 436 and p. 563). In Chapter 22, which presents a selection of problems and examples well calculated to stimulate readers, a certain proportion, fortunately not great, of the space seems to be devoted to an attempt to resolve the difficulties created by classifying ecological factors categorically as "density-dependent" (essentially coextensive with "biotic" in a more obvious classificatory scheme) or "density-independent" (physico-chemical).

The reviewer objects to the above classification on the grounds that density-independent factors, which are defined as destroying a constant percentage of the population regardless of population density, are probably inconceivable (except as they destroy 100 percent); that in Chapter 23 and elsewhere much conclusive evidence in adduced to show that alterations in population density are exceedingly important in limiting mortality caused by non-biotic (i.e., "density-independent") environmental factors, and that the terminology of density-dependent factors, such as predation, confuses even its enthusiastic users by confounding size of the population exposed to the factor with size of the other (predator) population. Thus on p. 371 we find a list of numbered generalizations indicating that when a prey population is large predation may be either large or small and that when the exposed population is small predation may be either intermediate or small.

Section III concludes with chapters on animal aggregations and the organization of insect societies, subjects in which the two senior authors are acknowledged authorities. These chapters not only provide the logical termination to a discussion of populations but they are

also the best summaries of the subjects known to the reviewer. Beginning with undercrowding, overcrowding, and natural cooperation they progress logically into territoriality, social hierarchies, and leadership, and finally develop the concept of a social organism in a persuasive manner.

Section IV consists of 162 pages devoted to the community and related multiple-species assemblages from the standpoints of "stratification," "metabolism," "periodism," "succession and development," and biogeography. Space will not permit a detailed examination of the intricacies and complexities of terminology which introduce difficulties into this section but the reviewer feels that the authors may have misinterpreted the common criticisms of ecological terminology. It seems probable that criticism may be directed less at the absolute number of terms than at the superfluity of terms that defy precise definition. The hope that in this definitive work there might be some precise usage of "community," "biocoenosis," "biome" and the like which would enable a student to recognize and delimit such units with assurance has not been realized. In fact the chief effort to simplify terminology seems to have been devoted to expanding the limits of terms to yield multiple synonomy. One could almost suspect malice when he reads on p. 568, "Such a cattle dropping is one of the habitat niches of the grassland floor, and may be termed a biotope, habitat, habitat niche, a microhabitat, biocoenose, or community without in any way doing violence to the realities of the situation. This microcosm. . . ." Student reaction to many parts of the book is a desire for a glossary and it seems likely that, had preparation of a glossary been attempted, the authors would have been led to more precise usage in many places.

Aside from semantic complications the section on communities is a mine of well integrated and carefully selected information, again summarizing diverse subject matter in a manner not available elsewhere.

The final section of the book is devoted to "ecology and evolution" and is an extraordinarily effective amalgamation of genetic and ecological principles. The scope of this section is tremendous and the reader lacking a *thorough* background in genetics may sometimes feel that he is reading a rapid-fire summary of conclusions either to be accepted on faith or to be regarded as abstracts each leading toward an extensive program of study. The emphasis of this section is on natural selection acting upon biological units which may commonly be more than individual organisms. The approach is convincing, even uncontestable, but on p. 694 where supraorganismic properties of human society are postulated it is pushed to an extreme unnecessary for the purposes of the volume. This postulate is supported by analogy solely, without discussion of possible selecting factors, relative rates of survival and fertility, or barriers to gene movement and with no attempt to define desirable objectives for "intelligent, artificial selection of social units." This latter may be an important oversight in discussing a species already under suspicion of living on capital resources.

In summary let us state our conviction that Principles of Animal Ecology supersedes all existing volumes on general or animal ecology, that it is an indispensable work for those who seek a broad understanding of biological phenomena generally, and that it will be a source of inspiration for research, speeding ecology toward a more mature and analytical future. Perhaps it is inevitable in such a comprehensive work that in the course of becoming unified it has become a somewhat difficult book, one which must be read in its entirety before the individual parts can become completely meaningful. This, together with its length and price, limits its field as a text but it is a reference book which every ecologist must possess.

The format is attractive. The illustrations, largely graphical, have in most cases been redrawn with improvements from the original sources. A very few such as one on p. 232, are confusingly labeled, and one on p. 559 might be used as a "not this" example in a text on graphical methods. However, the selection is in general excellent. The reviewer detected a few errors of a typographic or editorial nature, of which only two seem potentially confusing. On p. 433 the abbreviation $\mu\mu$ is twice used instead of $m\mu$ and on p. 637 the allometric (heterogonic) growth formula is incorrectly written as $Y = \log b + k \cdot \log X$ where "Y" should be written as "log Y."

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Concerning Human Evolution [1]

My introduction to this book came from a geneticist who wrote: "In several places Keith refers favorably to your work, and at one point (p. 60) makes a statement that will interest you greatly:

That groups of primitive humanity should be imbued with a team spirit, and should have

[1] **Keith, Sir Arthur.** 1949. A new theory of human evolution. New York: Philosophical Library. x + 451 pp. $4.75.

forged out of co-operation and competition a single and effective instrument to serve in their evolutionary advance, seems an almost trite idea, yet in all my reading I have come across only one author who has given it a clear expression —namely, Prof. W. C. Allee. As to the factors which are concerned in the natural production of new forms of organic beings, I find that I have more in common with him than with any other biologist, excepting his idea that evolution should culminate in making mankind into a single co-operative community."

This letter, dropped into the Editor's mail-box as an item of personal interest, immediately brought a copy of the book together with a request for a review. I began reading the attractive volume handicapped by favorable prejudice and stimulated by curiosity concerning Sir Arthur's reasons for not favoring the development of a world-wide cooperative human community. The hunt led through the entire volume with hope lasting almost to the end that there might be a lucid, concise statement of the author's position on this point comparable to his treatment of many others. The hunt lacked success, but somewhat later I shall try to suggest his possible reasons. I do not want to emphasize this point of disagreement when the author and reviewer have so much in common in that part of the book concerning which the reviewer has some right to advance an opinion. I am not an anthropologist and cannot judge the book from that point of view.

Having read the whole, it is easy to agree with the author's own estimate as given in the preface as follows:

Readers and critics, having looked at the first essay, in which my theory is outlined, having glanced at the synopses which preface each essay, and having read the summary given in the last essay, may be moved to say: Why, this is not a new theory; it is simply Darwin's theory extended, modified, and brought up to date! With such a verdict I will not quarrel; the foundation on which I have built is that laid by Darwin. But the theory of human evolution expounded in my text differs in so many things, both great and small, from that outlined in *The Descent of Man*, that I think it is entitled to be called "new." At least it is a new rendering of the Darwinian theory.

The core of Dr. Keith's theory is that from the very beginning evolving humanity was divided into a multitude of small separate co-operative groups that competed with one another. Again and again he emphasizes and documents his conviction that internal group affairs are ruled by a code of amity based in mankind on "love, affection, sympathy, fellow-feeling, mutual trust, faith, goodwill, mutual service, tolerance, charity, and loyalty." Contrariwise, intergroup human relations are equally firmly based on a code of enmity founded on "dislike, hate, illwill, distrust, suspicion, intolerance, deceit, treachery, contempt, envy, jealousy, and malice" (p. 101).

Competition between groups "favoured the tribes which were rich in co-operative qualities. It may be regretted," the author states (p. 13), "that Darwin did not lay greater emphasis on the part played by co-operation in his scheme of evolution. . . . He was quite aware so far as concerns human evolution, that co-operation was combined with competition."

The book contains 41 somewhat chapter-like essays. Each opens with a synopsis and closes with a list of selected references that have been cited in the text. Essays I–IV present evidence that early man lived in small isolated groups each anchored to a given territory; V–VIII discuss the mental qualities that keep members of a group together and those that turn them away from adjacent groups; XIV–XX are devoted to a study of the machinery of human evolution in regard to structural and functional changes; XXI–XXVI together with XVIII deal with bridging the gap between the highest anthropoid ape and man.

The remaining essays are devoted to "post-primal" development starting with the Caucasians who lived on the Iranian plateau about 9000 B.C. and ending with selected modern nations that have developed from that stock. These range from Jews, long stateless but held to be a race nevertheless, to the Caucasian "Yusanians" ("USA'ans" plus Y from Yankee!) who are said to be building a nation and a race on a continental scale—"a new phenomenon in the evolutionary history of mankind."

Apparently Sir Arthur Keith's conviction that human evolution should not culminate in the development of a "single co-operative community" is based mainly on the importance of competition between evolving human social units. Presumably from this approach the development of a single world-wide community might be feasible if we find other inhabited planets—say Mars and/or Venus—having populations with which we might compete on a global basis.

Another possible objection against a world-wide single human community was anticipated (p. 240) in my 1938 book, which Dr. Keith cited more than once with approval:

A thoughtful and sincere biologist may object that the world is too large an area for a successful co-operative unit; that we need units intermediate in size to allow for human evolution those advantages which Professor Wright [2] has demonstrated for populations intermediate in size [or the still greater advantages resulting

[2] **Wright, Sewall.** 1931. Evolution in Mendelian populations. Genetics **16**: 97–159. For later confirmation see: *Idem.* 1945. Tempo and mode in evolution. A critical review. Ecology **26**: 415–419.

from small interbreeding almost isolated colonies with occasional interemigration]. To such an objection one must reply that, as to the latter point, the maintenance of smaller co-operative and competing units within the larger one is part of the scheme as sketched. And to the first, that of the great size of the earth, it needs only to be mentioned that, thanks to recent improvements in transportation facilities, New York is in point of time as near the Orient as it was to Los Angeles in 1885; and there are few places on the globe as remote from Washington as was San Francisco before the Union Pacific Railway was built. In transportation and communication, and in community of essential human interests, the world is ripe for a workable international organization. (Allee, W. C. 1938. The social life of animals. New York: Norton.)

The argument is even stronger today than when first written.

Keith does not seriously consider the effect of human cooperation on a world scale in relation to the needed competition with viruses, bacteria, and other disease-producing organisms, or with parasites, or insects, which affect the welfare of man or of his domesticated plants or animals.

The book under review is honest, clearly written, and well documented. The author has taken care to give credit to the many men whose work and ideas he uses. The writing apparently was finished on the eighty-first birthday of its distinguished author. The reviewer hopes that he may have the vigor and the ability to produce a volume of comparable excellence at that mature age.

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Natural History of Marine Animals [1]

If Ecology *is* scientific natural history the MacGinities have written a book which should be of interest to ecologists. The book contains 31 chapters: The first twelve deal with the general problem of food-gathering, adaptation of animals to the sea (such as marine habitats, burrowing, etc.), variation and succession, geological records, and other phenomena. The next eighteen chapters take up in turn each phylum of animals and discuss habitat, adaptation, feeding and other habits, enemies, growth and regeneration, reproduction, commensalism, and various special topics. The last chapter discusses the relation of various land vertebrates to shore conditions, for example, the feeding by birds along the sea shore. Two short appendixes list the phyla discussed in the book, and their general habitats. There is an annotated bibliography of eleven titles. The index lists approximately 1,800 entries of which about 40 per cent refer to specific names, 40 per cent refer to common names of animals or structures, and 20 per cent refer to items, broadly interpreted, of an ecological content.

There are 282 figures: 85 line drawings and 197 photographs. 96 per cent of the photographs and 82 per cent of the line drawings are original, a very high percentage. About 70 per cent of the figures are judged to illustrate animals or structures; 30 per cent are ecological in that they show some relation of the animal to other animals or to the environment. Many of the fine photographs in the book are handicapped by mediocre reproduction; yet the pictures are well chosen and make their points as do the clearly executed line drawings. On the whole the book is attractively made up.

The MacGinities have not written this book for ecologists. They state that they had in mind two groups of people: laymen, and students and teachers of zoology. Whether it can have a wide appeal to laymen is open to some question. It is true that the MacGinities have done an admirable job of sticking to their promise made in the preface to keep the text clear of all unnecessary terminology and to define all technical terms as they are used. As a result, no intelligent person can fail to find the text both clear and readable. But the nature of the material is such as would appeal only to the rather serious layman who has already become familiar with the groups of invertebrates. If this is so, then one may ask whether the MacGinities could have saved much space given to descriptions of each of the phyla and have dug more deeply into their rich experiences with the natural history of these groups to give students and teachers of zoology their undivided attention. Take, for example, the short chapter on nematodes and chaetognaths. The only illustrations in the chapter are two photographs showing a nematode moving about within a living chaetognath. They are of interest to the student of invertebrates or of ecology, but are quite inadequate for informing a layman about the appearance or structure of the two groups. The text in this chapter is a brief description of the two groups which offers nothing new to the zoologist. Fortunately, this does not apply to those chapters in which the

[1] **MacGinitie, G. E., and Nettie MacGinitie.** 1949. Natural history of marine animals. New York: McGraw-Hill Book Co., Inc. Pp. 473; 282 figs., 6 × 9. $6.00.

MacGinities have much to offer from their own experiences. One may doubt whether a layman will have much interest in an animal like *Urechis*, that he is never likely to see. But anyone who has ever gone to Elkhorn Slough in California at 5 A.M. and has dug *Urechis* from the mud cannot help but enjoy the excellent material on the natural history of this animal and the frequent references to it in this book.

Dr. MacGinitie is well known to ecologists, particularly marine ecologists, for his original and significant observations and contributions to the ecology of our West Coast. And this book reflects the wide experience few but he could bring to a book on the natural history of marine animals. One may question small matters such as the use of various terms (such as symbiosis in the restricted sense of mutualism) or call attention to such trivia as the misuse of microphotograph for photomicrograph. None of these detract from the essential value of a book that, written for a different audience, does contain a great deal of material of interest to ecologists, particularly the feeding habits of marine invertebrates, a subject about which few people can be of as much help as are the MacGinities.

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The Pronghorn Antelope and its Management [1]

This is the sixth treatise on game species to appear under the auspices of the Wildlife Management Institute. It is an excellently printed volume, well illustrated with 70 photographs of high quality, a colored frontispiece by Walter Weber and another color plate reproducing an unpublished painting by Charles M. Russell.

This book presents a wealth of original observations, well organized and clearly stated. It is written with a light hand and will be equally palatable to sportsman and more technical reader. It is obviously aimed at both.

After a brief history of the species in America —its early abundance and later decimation— Einarsen treats of the many peculiar physical characteristics, behavior patterns, and food habits that make this strictly American species unique. The pronghorn antelope, averaging little more than 100 pounds in weight, has eyes as large as a horse, can detect the slightest movement of a coyote at four miles, has stronger leg bones than a cow of seven times its weight, and heart, lungs and trachea so large that it can attain tremendous speed even at high altitudes. One animal passed the car driven by the author at 61 miles per hour.

It is not surprising that such an animal should have a daily cruising range exceeding that of any other big-game species on this continent. The implications for agriculture and the impact civilization has made on the ecology of the pronghorn are well discussed. Although using range shared by cattle and sheep, pronghorn provide little competition for forage because their chief item of diet is sage—unpalatable to cattle but actually more nutritious than alfalfa. It is indeed encouraging to know that every western state now has at least a nucleus herd and that eleven have been able to open a shooting season in recent years.

The longest chapter is devoted to management —actually applied ecology—of pronghorn antelope. Einarsen shows here that in spite of the mobility of antelope they are slow to repopulate vacant range. This process is best accomplished by trapping, and transplantation of small bands to suitable unoccupied areas. The best means of hunting and the management of hunters also are thoroughly discussed.

Although interesting population and harvest figures are included, no real discussion of population turnover is attempted. One wonders just what the author thought along this line when he states, ". . . pronghorn deaths may often be classified as due to predation or disease, when actually they are due to natural causes."

Although hailed as a monograph it hardly deserves the title, for its treatment of many aspects of pronghorn biology is elementary at best, and seldom if ever are comparisons made with similar phenomena in other hoofed mammals. Such incautious statements as "There are few animals as adapt in effective displays" or "The collection of harems is not a common breeding characteristic among big game animals . . ." should have been caught by the editor. The bibliography is not what one would anticipate in a monograph; it is brief and omits several references cited by the author as well as other well-known works on the pronghorn that are ignored in the text—e.g. Pocock ('05), Mearns ('07), and Nichol ('42).

In spite of these shortcomings, Einarsen's book is one every ecologist will want to read for an interesting account of this little-known species. Students of behavior will want to read about Einarsen's observations of such phenomena as the establishment of nurseries by lactating females. And the great band of ecologists engaged in game research and management will find good ideas on the management of hunters as well as pronghorns.

William H. Elder
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[1] **Einarsen, Arthur S.** 1948. The pronghorn antelope. Washington, D. C.: The Wildlife Management Institute. Pp. xvi + 238. $4.00.

Birds of Concord [1]

It is a rare event when population ecologists have access to historical data accumulated over relatively long periods of time. The study of birds, however, has been seriously pursued since the eighteenth century and, in some instances, records have been consecutively maintained. In fewer instances these records appear to be competent. Ludlow Griscom has delved into the records pertaining to the birds of the Concord area of Massachusetts. These have been kept since the time of Thoreau by such able observers as Thoreau himself, by Brewster, by Browne, by Faxon, by Maynard, to name but five. Study of these data furnishes the core of the book here under review.

"Birds of Concord" falls into two sections. The first portion is a study of the historical records in relation to population trends. The second portion constitutes a synoptic list of the birds of the area with short paragraphs on the population changes of each species. Included in the first part is a brief consideration of the impact of the rise of ecology upon ornithology. The author then surveys the effects of the various environmental factors upon bird populations. Of particular interest are the data dealing with the impact of white man's civilization on the avifauna of primeval New England and the changes that ensued when destruction by man altered the habitats available to birds. Among the changes itemized and discussed, and produced by man directly or through his introduction of alien fauna and flora, are the effect of the English Sparrow on the native birds; the introduction of insects (particularly caterpillars and their relationship to cuckoo populations); the eradication of marshlands, and, finally and most important, the repetitive burning and lumbering of forests. Climate and its relation to variations of bird populations is analyzed very thoroughly. In addition to such synecological considerations a section is devoted to autecology. The bibliography is short but pertinent.

As is the case with Griscom's previous publications, this book is written lucidly and precisely with a minimum of verbosity and a maximum of clarity. Because the book is more or less of a pioneering work in the use of historical data for bird population studies, the author's conclusions cannot be readily appraised. One statement that may be brought into question is the remark that ". . . the reason why Egrets never occurred in the Sudbury meadows of the Concord region until after 1920 is that there were not enough Egrets." Since no records earlier than 1907 are given in the second part of the book and since only vague references are included in the first portion, one wonders if this is truly the case. Certainly Thoreau, who observed birds before the plume hunters began to decimate the Egret populations, would have been expected to notice these birds if they were about.

Philedelphia ornithologists may be inclined to question, and consider as either provincial or jingoistic, Griscom's remark that Concord has ". . . a greater number of competent and nationally known ornithologists than any other corner of the New World." It would be of great interest to have a study similar in scope to the present one performed upon the birds of the Philadelphia region—an area that has had such well-known ornithologists as Audubon, Wilson, Cassin, Say, Coues, and a host of others down to the present day members of the Delaware Valley Ornithological Club. Griscom suggests that similar studies could be profitably undertaken in the Old World.

Ornithologists and population ecologists will find much of value in this volume while Concord naturalists will obviously like the historical discussion and may perhaps be pleased that their justly famed region has taken on new luster.

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[1] **Griscom, Ludlow.** 1949. Birds of Concord. Cambridge, Mass.: Harvard University Press. Pp. 340. $5.00.

Studies in Freshwater Fishery Biology [2]

This text for the college student of biology which first appeared in two mimeographed editions (1947 and 1948) is now available in a much more compact and usable form in lithoprint. The book is an outgrowth of the author's courses in fishery biology given at the University of Michigan since 1940. Although primarily a field and laboratory manual it has carefully selected bibliographies for each phase of the subject.

Sources of fish literature are first presented by a survey exercise followed by outlines for the various studies in life history, population estimation, creel census, pathology, pollution, laws, artificial propagation, biological surveys and their application to improvement or extension

[2] **Lagler, Karl F.** 1949. Studies in freshwater fishery biology. Ann Arbor, Michigan: J. W. Edwards. Third revised edition. Pp. v + 231, 74 figs. $4.00.

of the environment. A study of local commercial fisheries is outlined with a list of questions to be answered by the student from his observations. The final exercise is one which should have strong appeal—fresh water sport fishing—including all methods employed in winter as well as summer. Six appendices devote special consideration to the body-scale relationship, and, for various game fish, tabular summaries from the literature of average and calculated lengths, coefficients of condition, reproductive periods, and fecundity. Commonly used conversion tables and a reproduction of Embody's stocking table for trout streams conclude this section.

The author does not consider this publication a text-book but rather a series of library, laboratory and field exercises designed to acquaint the student with the methods currently employed in freshwater fishery research and in the interpretation of the results in terms of management. Reproduction of photographs is excellent and the type is large and clear. This pioneer work should have wide acceptance in all training centers for freshwater fishery biologists and fish managers.

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Michigan Department of Conservation,
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BOOK NOTICES

Bates, Marston. 1949. The natural history of mosquitoes. N. Y.: The Macmillan Company. Pp. xv + 379. $5.00. Doctor Marston Bates of the Rockefeller Foundation has written an excellent book. The account is valuable, of course, as a discussion of the ecology of mosquitoes and, in this respect, lives up creditably to its intended objective. But the book has a value beyond this. It illustrates how much the ecologist can learn through comprehensive field and laboratory study of a single group considered in relation to its ecosystem. Bates drew on varied sources, including a rich personal experience, in organizing his manuscript and then assembled his story in readable, and critical, form. By no means the least attribute of the book is the repeated insistence that all is not known. Many fascinating problems for future work are pointed out along the way. The book should be placed in the hands of students as an illustration of how an ecological program can be developed.

After an appropriate introduction, graced with a tinge of philosophy, Doctor Bates considers the environment of the adult mosquito; the problem of survival and dispersion; the matter of behavior, especially in connection with mating and feeding, and the problems centering around development. Then follows a treatment of the larval stage and one finds such topics as "The larval environment," "The physiology and behavior of larvae," "The biological environment of the larva," and "The classification of larval habitats." After briefly summarizing certain facts pertaining to the pupa, the mosquito in relation to other organisms, and as a vector of disease, is examined. Questions of mosquito distribution, speciation, and classification constitute three chapters. The volume concludes with "Techniques in mosquito study" and "The strategy of mosquito research." In the latter chapter this interesting comment appears: "The academic biologists are thoroughly aware of the importance of detailed study of population dynamics, of quantitative measurement of the forces that surely govern the process of organic divergence. If they can be interested in utilizing the rich material that lies available in mosquito studies, perhaps as a by-product of the investigations, they may produce contributions to that other area of scientific strategy, the attack on the problems of human disease."

There is an appendix listing the species of mosquitoes; a first-rate bibliography, and what appears to be an adequate index. [T. P.]

Steinhaus, Edward A. 1949. Principles of insect pathology. N. Y.: McGraw-Hill Book Co., Inc. Pp. xi + 757. $8.00. Biologists are already in debt to Dr. Steinhaus for his useful summary published in 1946, "Insect microbiology." The appearance of "Principles of insect pathology" increases this debt. Taken in conjunction, the two volumes summarize a wealth of information about insects. In fact, along with such important ventures as Wigglesworth's "The principles of insect physiology" and Snodgrass' "Principles of insect morphology," we are now accumulating a book library in the English language which will go a long way to prove that insects, after all, are really animals with a basic and complex biology and not exclusively the property of taxonomists, important as are the researches of the latter workers. The present book is viewed by its author as a text. But it is a source-book as well and much broader in its scientific implications that the title might imply. The organization is essentially systematic, the chapters stressing pathology in terms of causative agents. The agents may be physical and chemical, or organismic. Chapters are devoted to resistance and immunity, to symptoms and pathologies, and to bacterial, fungous, virus, protozoan, and nematode, infections. The final chapter with the title "Applied insect pathology and biological control" has a strong ecological flavor. Its theme, simply put, is "disease as a factor in ecology"—its attack, epidemiological and populational. While not a comprehensive statement about the subject (as indeed would be inappropriate in this book), it is refreshing to find this point of view championed in a volume on pathology.

"Principles of insect pathology" is, unquestionably, a welcome addition to the literature. [T. P.]

Moog, Florence. 1949. Structure and development of the vertebrates. A manual for an integrated course in comparative anatomy and embryology. N. Y.: Prentice-Hall, Inc. Pp. xi + 170. This manual is novel in its approach and completely sound in its basic pedagogy. What it does at the vertebrate level is to treat morphology and ontogeny more or less simultaneously as two aspects of the same thing rather than as disparate units. Certain quotations help to describe the scope of Doctor Moog's venture. "This book is designed to serve the needs of a course in which the usual subject matters of comparative vertebrate anatomy and comparative vertebrate embryology are integrated into a single sequence. Such a course has been taught at Washington University. . . . Its results, in improvement of student interest and comprehension, have been so favorable as to induce us to abandon permanently the traditional separation between anatomy and em-

bryology. . . . Students should be thoroughly grounded in the essentials of embryonic form and development before plunging into the complexities of comparative anatomy itself. This is what this book aims to do."

The volume is excellently illustrated and the directions are clearly presented. In fact, Doctor Moog writes so very well that one is surprised to find on an early page such a platitude as: "To most of us, the human body is the most fascinating structure in the biological realm." The statement has validity, of course, and without question the book will go a long way towards furthering such a view. But should not the student *discover* this opinion for himself as the course proceeds rather than having it pointed out even before he fingers his first *Ammocetes?* [T. P.]

Wright, Albert Hazen, and Anna Allen Wright. 1949. Handbook of frogs and toads of the United States and Canada (third edition). Ithaca, N. Y.: Comstock Publishing Company. Pp. xii + 640. $6.50. Earlier editions of this attractive handbook appeared in 1933 and 1942. Though not markedly altered, the present edition stresses to greater degree the testimony of far-flung herpetologists and amateurs in reporting upon the natural history of the forms under consideration. The authors discuss this feature in the Preface: "In all our portrayals we have sought to emphasize the living animal by photographs from life, by color descriptions from life, by journal notes from the field, and particularly by excerpts from others' work pertaining to live frogs. In many regions we have been transitory visitors and the resident naturalists can tell a more complete story. Our notes and notes of others, which in the two earlier editions were merged under the heading 'Notes,' are here expanded and designated 'Journal notes' and 'Authorities' corner.'"

The book is nicely printed and bound and is replete with excellent half-tones.

Chandler, Asa C. 1949. Introduction to parasitology (eighth edition). N. Y.: John Wiley & Sons, Inc. Pp. xii + 756. $6.00. This well-known text on parasitology has now entered its eighth edition. It is only necessary in this notice to call attention to the major alterations that have been incorporated. The author discusses these in the Preface as follows: "The rapid advances in knowledge in the field of parasitology have made it necessary to revise and rearrange this book every four or five years. In the five years that have elapsed since the seventh edition was written, more advances have been made than in any similar period since the book was first published, so again it has been entirely rewritten, with changes on every page. A few important alterations or additions have been made. A new section has been added on arthropod-borne bacteria, rickettsias, and filtrable viruses to give the student a more comprehensive view of these disease agents and their relations to their vectors than can be gathered from disjointed discussions of them under their individual vectors. Another new section has been added to deal with insecticides and repellents. The Acanthocephala have been segregated into a separate chapter. New keys to some of the arthropod parasites have been added. References to and consideration of parasites of domestic animals have been greatly extended. Most of the illustrations have been improved or are entirely new."

Bovey, Martin. 1949. The saga of the waterfowl. Washington: The Wildlife Research Institute. Pp. xiv + 141. $5.00 "This book is merely a brief account of what our forefathers have done and we ourselves are doing to bring about the end of American waterfowling. There is not one new idea, not one fresh thought in this book. Every word of it has been written before. Nevertheless, it must be written again, for the story has not yet been learned and taken to heart by a sufficient share of our gunners" (from the Foreword).

This handsome volume tells its story by means of 71 splendid, full-page photographs. Each picture appears as a right hand page and is faced on the left with an appropriate sentence of commentary. Every photograph displays technical skill and not a little artistry and some have considerable ecological interest. The major theme is that habitats, water-tables, and cover should be cherished and that sound game laws should be enforced and respected.

Barghoorn, Elso S. *et al.* 1949. The Boylston Street fishweir II. Edited by Frederick Johnson. Andover, Massachusetts: Papers of the Robert S. Peabody Foundation for Archaeology, vol. 4, no. 1. Pp. x + 133. $2.00. An extension of the report published in 1942. The discovery of axe-sharpened stakes 40 feet or more below the present ground surface has led to a search for further information about the people who inhabited the Boston area at least 3000 years ago. Excavations carried out for that purpose have provided opportunity for investigation in many other fields, all of which may ultimately contribute to a better knowledge of the topography, climate and vegetation in earlier days. Elizabeth G. Lawrence.

Beadle, N. C. W. 1948. The vegetation and pastures of western New South Wales with special reference to soil erosion. Sydney: Department of Conservation of New South Wales. Pp. 281. Further desolation of large areas of

dry grazing land by wind-erosion can be prevented only by regeneration and maintenance of adequate vegetation. This book prepares the way for an attack on that problem by providing a detailed study of the region, including history, topography, climate, soils, and vegetation types, and concluding with a discussion of succession, climaxes, and the interrelationships of plant communities. Elizabeth G. Lawrence.

Dean, H. L. 1949. Biology of plants. Dubuque, Iowa: Wm. C. Brown Co. Pp. 265. $2.25. Laboratory exercises for a two semester course in college botany, with many drawings, diagrams, and tables to be labelled or otherwise completed by the student. Elizabeth G. Lawrence.

Chapman, Herman H. and Walter H. Meyer. 1949. Forest mensuration. New York: McGraw-Hill Book Co. Pp. xiii + 522. $5.00. The content of "Elements of forest mensuration" by Chapman and Demeritt, 1936, has been completely revised and extended to include new techniques. It is designed to serve as a text for either elementary or advanced students. Elizabeth G. Lawrence.

Huber, Hans, editor. 1949. Carte de la végétation de la Suisse. Berne: Commission Phytogeographique de la Société Helvétique des Sciences Naturelles. U. S. distributor, Grune and Stratton, Inc., 381 4th Ave., N. Y. 4 sheets, 1:200,000. Sheet 1, NW quarter; sheet 2, NE; sheet 3, SW; sheet 4, SE. Paper, each s Fr 12.—; linen, s Fr 16.—.

Vegetation types, natural and cultivated, are shown in color superimposed on a topographic map of Switzerland. Key symbols are interpreted in German, French, and Latin. Elizabeth G. Lawrence.

Jacquet, Jean. 1949. Recherches écologiques sur le littoral de la Manche. Les prés-salés et la spartine de Townsend. Les estuaires. La tangue. Encyclopédie Biogeographique et Écologique, V. Paris: Paul Lechevalier. Pp. iv + 374. 2500 fr. Taxonomy, anatomy, geographic distribution, and ecology of *Spartina Townsendi,* with a discussion of many related problems of oceanography and littoral biology. Elizabeth G. Lawrence.

Kramer, Paul J. 1949. Plant and soil water relationships. New York: McGraw-Hill Book Co. Pp. xiii + 347. $4.50. Directed to teachers, investigators, and students in all fields of plant science, this advanced text attempts to discuss all the factors which influence the rate of absorption of water, and incidentally of solutes, from the soil by plant root systems. Elizabeth G. Lawrence.

Nuttonson, M. Y. 1949. Ecological crop geography of Germany and its agro-climatic analogues in North America, and Agricultural climatology of Japan and its agro-climatic analogues in North America. International Agro-climatological Series, studies no. 8 and 9. Washington, D. C.: American Institute of Crop Ecology. Pp. 36 and 20. This series of studies represents an outgrowth of plant-introduction problems brought about by the urgent need for speedy rehabilitation of war-devastated areas. Their purpose is to promote research in crop ecology, particularly as it affects the exchange of plants among the agricultural areas of the world. Elizabeth G. Lawrence.

Stoeckeler, E. G. 1949. Identification and evaluation of Alaskan vegetation from air photos with reference to soil, moisture and permafrost conditions. A preliminary paper. St. Paul, Minnesota: Dept. of the Army, Corps of Engineers. Pp. viii + 103. $2.00. Ground reconnaissance in many parts of Alaska in combination with study of vertical aerial photographs reveals to what extent air photos can be used in the prediction of soil and permafrost conditions from vegetation and topographic features. Elizabeth G. Lawrence.

U. S. D. A., Forest Service. 1948. Woody-plant seed manual. Misc. Publ. no. 654. Washington, D. C.: U. S. Govt. Printing Office. Pp. vi + 416. $2.75. A compilation of information on all phases of seed handling, from seed development through seedling characteristics, covering 444 species of trees and shrubs potentially valuable in such fields as reforestation, shelter belt planting, erosion control, wild life management, and horticultural practice. Elizabeth G. Lawrence.

Van Steenis, C. G. G. J., editor. 1948. Flora malesiana. Series 1, Spermatophyta, vol. 4, part 1. Batavia, Java: Noordhoff-Kolff N. V. Pp. xl + 39. Price provisionally one guilder Netherlands currency for 16 printed pages, including postage. U. S. agent, Chronica Botanica Co., Waltham, Mass. The first published part of what is designed to be a complete but concise botany of the Malaysian Archipelago, to appear in about 30 volumes, at the rate of about 240 pages each year. It is to be an illustrated systematic account of the flora, including keys, descriptions, bibliography, synonymy, distribution, and ecology of wild and commonly cultivated plants. Elizabeth G. Lawrence.

Vestal, Arthur G. 1949. Minimum areas for different vegetations, their determination from species-area curves. Illinois Biological Monographs, vol. 20, no. 3. Urbana, Illinois: University of Illinois Press. Pp. vi + 129. $2.00 paper, $3.00 cloth. This book offers a simple

means of comparing different communities or different stands with respect to number of species present in equivalent "reference areas." The reference area for any vegetation type is ascertained by locating a point on the species-area curve of that vegetation by a method which involves certain ratios. About 240 examples of vegetation in many parts of the world are analyzed, the reference areas found ranging widely from about 0.1 milacre for lichen communities to a maximum of 21,650 milacres for a tropical river forest. Elizabeth G. Lawrence.

Davis, Darrell Haug. 1948. The earth and man. Revised edition. The Macmillan Company. Pp. xxiv + 696. $5.50. This revised edition is certainly an excellent beginning college geography text. It rates so primarily because it is dynamic in approach and considers past, present and future factors dealing with human populations. It reads interestingly, and the extensive use of good illustrations adds to its effectiveness. Many maps, primarily concerned with climatic conditions, are also included in the text.

The Earth and Man deserves reviewing in this journal, however, because of the large amount of ecological material presented. This is oriented towards man, as the title indicates but, of necessity, has other applications as well, largely in relation to conservation and plant ecology. Davis states as his theme ". . . the [physical] environment is a passive, not an active agent; it permits but it does not compel."

Physical factors are treated extensively. This treatment affords adequate reference material on aspects of climatic elements, soils, water supply, and topography for ecology students. The weather and soil maps alone could be quite useful.

Biotic factors are not dealt with in any detail. They are evident, of course, in discussions of conservation and in one relatively long section on plant communities. The latter is a concise treatment of the subject and creates an overall general picture without encumbering the mind with species names.

Conservation problems are apparent throughout and are realistically described in relation to their importance to man's cultural development. It is a pleasant change to see these problems discussed, not *per se,* but as they occur in the course of man's activities and evaluated in that light with accompanying methods as to how they are, or are not, being overcome. [Marian Burton Frank.]